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Schinus in Successional Ecosystems of Everglades National Park

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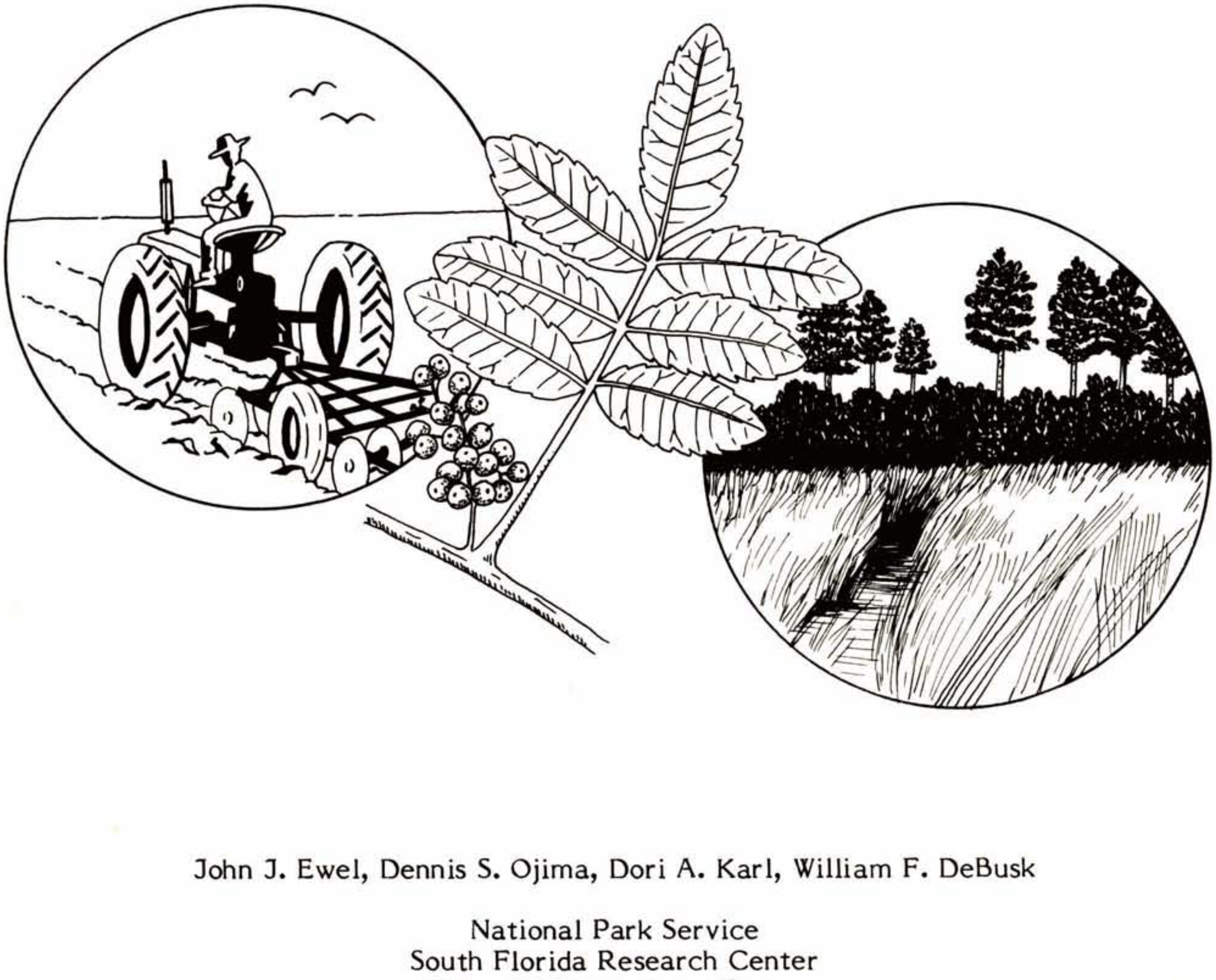

John J. Ewel, Dennis S. Ojima, Dori A. Karl, William F. DeBusk

National Park Service
South Florida Research Center
Everglades National Park
Homestead, Florida 33030

August 1982

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Ewel, John J., Dennis S. Ojima, Dori A. Karl, and William F. DeBusk. 1982. Schinus in Successional Ecosystems of Everglades National Park. South Florida Research Center Report T-676. 141 pp.

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ACKNOWLEDGEMENTS

In Everglades National Park we were assisted by many staff members, especially those of Resource Management working under the direction of Joseph Abrell and Robert Doren, and the Vegetation Ecology research group, working under the direction of Lloyd Loope. George Avery's assistance in plant identification was especially valuable. The Homestead Agricultural Research and Education Center of the University of Florida's Institute of Food and Agricultural Sciences provided important logistical support. Insects were identified by entomologists of the Florida Department of Agriculture and Consumer Affairs, Division of Plant Industry, Gainesville.

Others who contributed directly to the research included: Faye Benedict, Cory Berish, Chantal Blanton, Becky Brown, Cody Claxton, Vicki Dunevitz, John R. Ewel, Katherine C. Ewel, George Fuller, Dawn Green, Lee Jacobs, Julia Johns, C. Bruce Johnson, Alma Lugo, Sonia McDaniel, Carolyn Michaud, Edafe Oddo, Doris Randolph, Grace Russell, Alan Shaw, James Snyder, Patricia Veno, Robert Whelan, and Kenneth Young.

INTRODUCTION

The extreme southern 10% of peninsular Florida is, in many ways, a biologically unique environment. The landscape is geologically young, the topography is flat, and the climate is the most tropical of any part of the continental U.S. The vegetation of the southwest portion is dominated by mangrove forests, which occupy more area here than in all other parts of the U.S. combined. The central portion is triangular, with its apex pointed south. It is covered by a mosaic of wetlands: glades, prairies, marshes, and ponds. This area is dominated by herbaceous vegetation, but forests--locally called tree islands, bayheads, strands, hammocks, and domes--are interspersed throughout. The third portion is South Florida's "mountainous" region: the Miami Rock Ridge, which sweeps along the southeast coast, and curves inland (and into the Everglades National Park) just before it reaches the southernmost extent of the peninsula. This ridge, composed primarily of oolitic limestone, never attains an altitude of 10 m above sea level. The Miami Rock Ridge was once dominated by pinelands interspersed with broadleaved forests called hammocks. Today, however, the Ridge is almost completely urbanized except along its western and southern fringes, where it is used for agriculture: primarily production of winter vegetables.

The Miami Rock Ridge peters out in the Everglades National Park, near the southern apex of the seasonally-flooded-wetland triangle. Some of the lands near this juncture are in near-natural condition, and include some of the best examples of pinelands, prairies, and tropical hammocks in Florida. Much of this land, however, was farmed. All of it is now part of Everglades National Park, and no farming has been done in the area since July, 1975. Most land that was released from farming prior to 1950 has reverted to vegetation that is very similar to that which occupied the site before it was farmed. The advent of new technology during the 1950's resulted in more drastic site preparation, however, and the substrates were dramatically modified.

The technique of greatest site impact was rock plowing, whereby tractors and plows crush the limestone into small particles and mix it with any overlying marl or organic soil that might be present. A new soil, about 20 cm deep, is thus created. It is mechanically arranged into elevated rows, where crops are planted, separated by furrows. Agricultural practices include careful management of water (through drainage, irrigation, and use of plastic mulch), nutrients (through fertilizer applications), and pest control (through applications of herbicides, fungicides, nematicides, and insecticides). The substrate, even after rock plowing, is not an especially good soil for plant growth, but is better for crops than the soil and rock that underlie the native plant communities. Farming can be lucrative here primarily because high-value crops can be produced in the winter.

When rock-plowed lands are released from farming, they are quickly colonized by dense, diverse plant growth. One striking fact about the vegetation that recolonizes rock plowed glades and prairies is that it often develops into a forest, rather than into the herbaceous community that occupied such sites before farming. The farming produces a new substrate: one that is deeper, better drained, better aerated, and possibly more nutrient-rich than the pre-farming soil. Many of the plants that appear in the post-farming successional vegetation are mycorrhizal, i.e. their roots are symbiotic with certain fungi that aid in nutrient uptake (Fig. 1). Mycorrhizal plants are uncommon in the seasonally flooded glades, prairies, and marshes that occupied these sites before farming because the fungi are obligate aerobes, i.e. they require oxygen. Rock plowing, however, changes the substrate in ways that permit mycorrhizal fungi to survive, and this opens the area to colonization by plants that would have otherwise been unable to grow there.

One important colonizer of these rock-plowed lands released from farming is an exotic tree, schinus, that dominates vast areas of successional forest, even on lands that have not been farmed for more than 30 yr, and were never rock plowed. Because it is an exotic species; because it forms extensive, dense stands; and because it poses a potential threat of invasion into nearby native plant communities; schinus is of great concern to those charged with the management of Everglades National Park.

Schinus

Schinus terebinthifolius Raddi is 1 of about 28 species (Tomlinson 1980) in the Central and South American genus Schinus of the family Anacardiaceae. It is an extremely variable taxon, and Barkley (1944) discussed 4 varieties: acutifolius, Pohlianus, Raddianus, and rhoifolius, in addition to the "typical" form, Schinus terebinthifolius. However, field separation of the varieties is difficult (Barkley 1944, Campbell et al. 1980), and the South Florida populations have not been classified to the variety level. In the U.S. several common names are used for this species: Brazil peppertree (or Brazilian pepper or peppertree), Florida holly, and Christmas-berry. It is not a "pepper", it is not a "holly", and its fruit is not a "berry" (it is a drupe). In this report the generic name is decapitalized and used as a common name, as this is how the taxon is normally referred to by researchers and resource managers in South Florida. It is most commonly pronounced "shynus", but perhaps more correctly "skynus".

The anatomy and morphology of schinus were described by Oliveira and Souza Grotta (1965), and general botanical descriptions are in Barkley (1944), Little et al. (1974), Morton (1978), and Tomlinson (1980). Schinus is a compound-leaved, evergreen tree that reaches heights of about 13 m. It has a multiple-stemmed trunk, and its branches do not readily self-prune, but stay attached to the trunk and form a nearly impenetrable tangle that surrounds the tree to ground level. It sprouts vigorously from trunk and roots, even if undamaged (Woodall 1979a). Schinus is dioecious (i.e. it has male and female flowers on different individuals); male trees bear more flowers than do female trees. Campbell et al. (1980) examined 31 herbarium specimens (most identified to variety) in Brazil, and determined that collections of flowering schinus had been made in every month except May, June, and September. More flowering specimens (7) were collected in March than in any other month. Seven flowering specimens had been collected in October, the month when schinus flowering peaks in South Florida. In São Paulo,

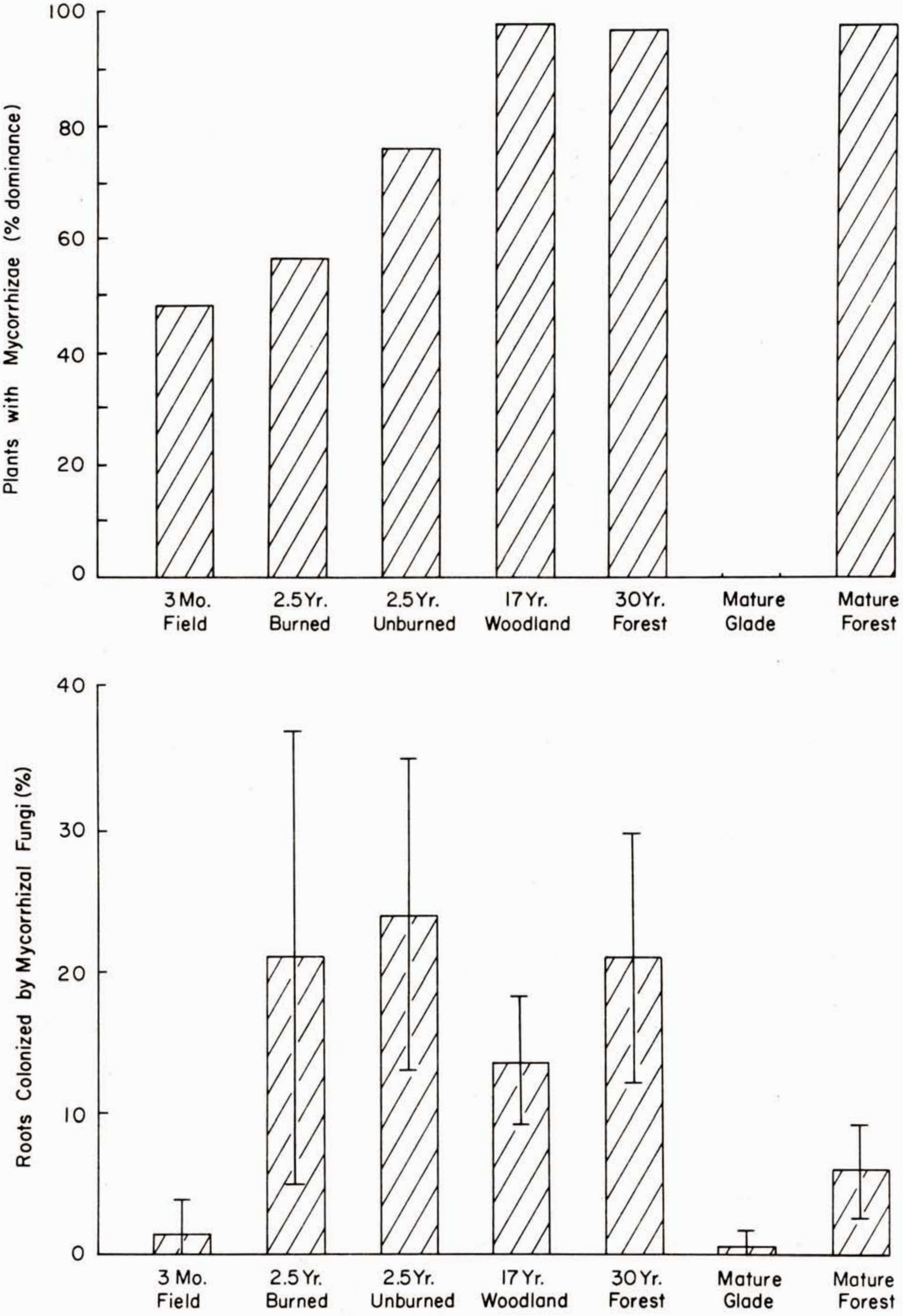


Fig. 1. Mycorrhizal status of plants on farmed and unfarmed sites in Everglades National Park. After Meador (1977).

Brazil, schinus blooms in March and April (Oliveira and Souza Grotta 1965), months when we seldom observed flowering in Everglades National Park. However, Morton (1978) reported that, in South Florida, there is no month when specimens cannot be found in bloom. Its fruit is a drupe, about 0.5 cm in diameter, and bright red when ripe.

Schinus may be allelopathic (i.e. it may release chemicals into its surroundings that inhibit the growth of competing vegetation) (Gogue et al. 1974), and it, in turn, is subject to allelopathy from Myrica cerifera (wax-myrtle), a common native shrub (Dunevitz and Ewel 1980). The foliage and fruits have a pungent turpentine odor, and Campbell et al. (1980) report that the odor is restricted to female trees. (We were unable to confirm this, but did not design a statistically valid test.) The plant has a long history of use in folk medicine in Brazil (see Morton 1978, plus references cited by Oliveira and Souza Grotta 1965). Morton (1977, 1978) called attention to the skin and respiratory irritation that schinus causes some people. Its recent use as a spice ("pink peppercorn") in gourmet restaurants is cause for concern (Salamon 1981).

The species is a native of Argentina, Paraguay, and Brazil, where it occurs in the states of Minas Gerais, São Paulo, Paraná, Rio de Janeiro, Rio Grande do Sul, and possibly others. It is found in a variety of habitats, ranging from sea level to >700 m. In its native range it is a sparse species, and never attains the dominance that it acquires in some of the places where it is a naturalized exotic. Schinus has been introduced, and become successfully naturalized, in >20 countries, and its range now forms 2 circum-global belts, 1 in the northern hemisphere and the other in the southern hemisphere, both concentrated at latitudes 15 to 30°. In Panama and Singapore its naturalized range approaches to within 10° of the equator, but schinus seems to be primarily a subtropical species.

In the U.S. schinus is found in southern Florida, southern Arizona, southern California, Hawaii, and in the Commonwealth of Puerto Rico as well as St. John, Virgin Islands (Little et al. 1974). Although it is an aggressive colonizer in South Florida and Hawaii, it has never become widely naturalized in southern California, where it is widely planted as an ornamental. Its lack of success in southern California was attributed to the short period of ample soil moisture, which is not long enough for germination and root establishment (Nilsen and Muller 1980). It was intentionally introduced into South Florida for use as an ornamental, and the date of first introduction is reported as 1898 (Morton 1978) or 1891 (Workman 1979). However, Barkley (1944) examined a Missouri Botanical Garden herbarium specimen collected from a cultivated plant in Florida by Rugel in 1842-1849, so the species was in Florida about 50 yr before it was "officially" introduced.

Even though schinus has been in South Florida since the last century, it did not become a conspicuous dominant in the area until after 1950. For example, Davis (1943) did not mention it, even though he was an especially keen observer. It successfully colonizes several native plant communities, especially the pinelands that occupy non-urbanized remnants of the Miami Rock Ridge (Loope and Dunevitz 1981a). It also invades hammocks, and forms extensive stands in the mangrove forests of Everglades National Park, especially in areas severely disrupted by hurricanes (I. Olmsted, Everglades National Park, pers. comm.). However, it most aggressively invades areas disturbed by human activities (Alexander and Crook 1973, Koepp 1979). It is common along roadsides, on powerline rights-of-way, and on canal banks. Its most common South Florida habitat, and the one studied as part of the research reported here, is fallow farmland.

This Report

This report describes research findings based primarily on field work conducted from March, 1978 until January, 1981. The 2 sections that follow describe the study sites and their hydrology. These are followed by 8 sections dealing with the autecology, silvics, population biology, and community ecology of schinus. Topics covered in these 8 sections include: phenology, pollination, dispersal, germination, seedling dynamics, seedling growth and survivorship, invasibility, and stand structure. After the 8-section description of the ecology of schinus, there are 2 sections dealing with schinus control: 1 deals with herbicide tests and the other covers stand conversion, especially the technique of matricide. The penultimate section deals with seed fluxes among plant communities and soil seed banks. The final section summarizes some of the important conclusions that emerged from the research, with special emphasis on those findings that have direct implications for management. Plant nomenclature follows Long and Lakela (1971) and Avery and Loope (1980b).

STUDY SITES

The research was conducted in the Everglades National Park, Ranges 36 and 37 East, Township 58 South, in southwestern Dade County, Florida (approximately 25° 20' N and 80° 40' W). Descriptions of the natural features, including the vegetation, typical of the general area are in Davis (1943), Egler (1952), Robertson (1955), Craighead (1971), Alexander and Crook (1973), and Wade et al. (1980). Soils of the area were mapped and described by USDA (1958).

Most study sites were located in the area of the Park referred to as the Hole-in-the-Donut, a 6,883 ha former in-holding, more than half of which was once farmed. The area, its land use history, and its vegetation are described in Hilsenbeck (1976b) and Resource Management Staff (1976). A substantial portion (1,900 ha) of the Hole-in-the-Donut was released from farming between 1973 and July, 1975, when the Department of the Interior made a major effort to acquire all Hole-in-the-Donut inholdings (R. Doren, Everglades National Park, pers. comm.). These lands were 80% wet prairie, 9% pineland, 7% sawgrass prairie, 2% hammocks and bayheads, and 2% ponds (Hilsenbeck 1976b).

The 3-year research program involved 15 kinds of field studies, and these were conducted at the 23 sites shown in Fig. 2. The studies conducted at each site are listed in Table 1.

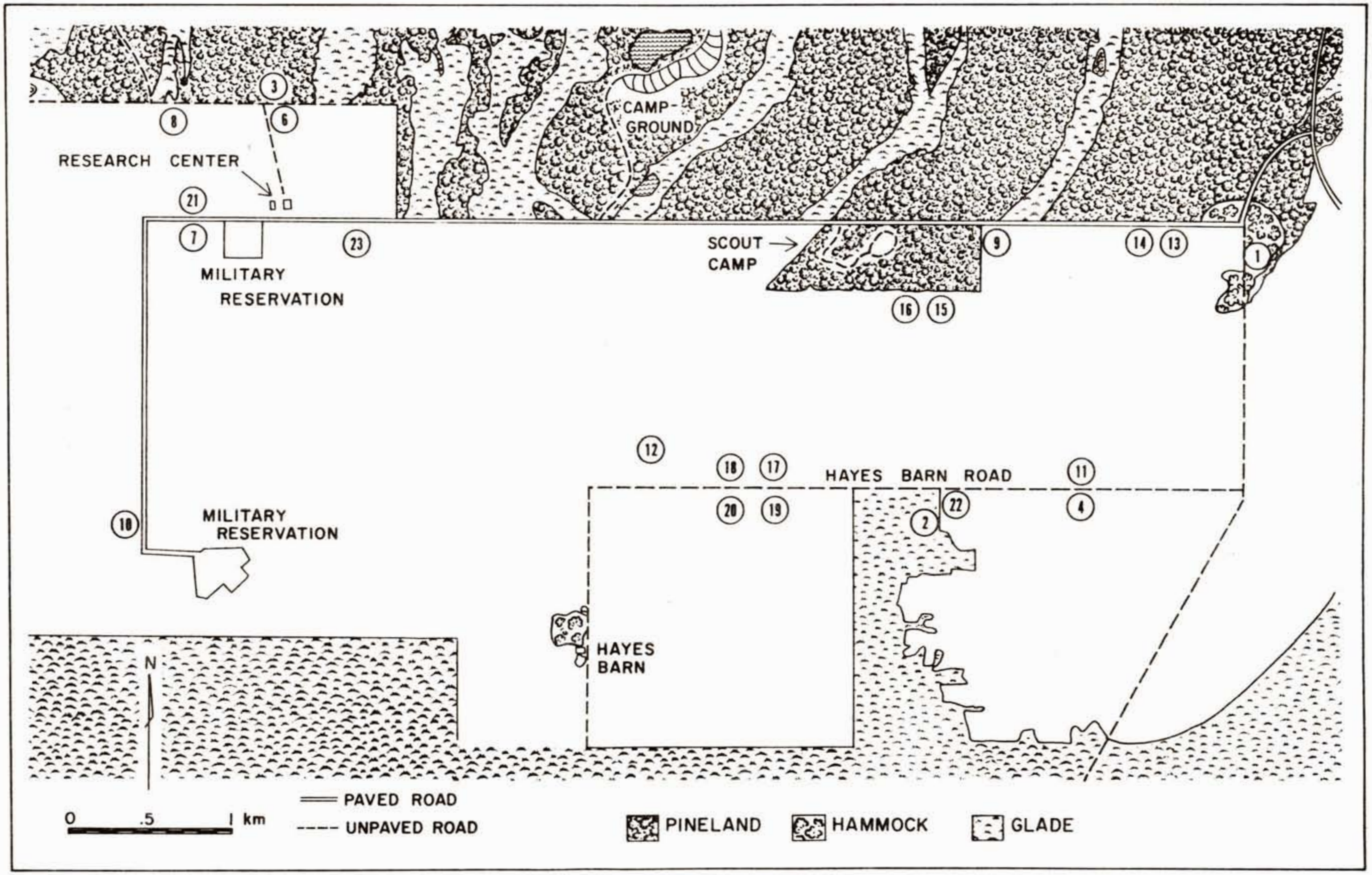


Fig. 2. Location of sites within the study area. Numbers correspond to studies listed in Table 1. Site no. 5 (old schinus forest no. 2) is off the map, 3.5 km ESE of site 1. Unshaded areas were farmed after 1950.

Table 1. Study sites and studies conducted at each. Locations are shown in Fig. 2.

	NUMBER ON MAP	WATER DEPTH	SURFACE FLOODING	PHENOLOGY	POLLINATION	DISPERSAL	SCHINUS SEEDLING DYNAMICS	SEEDLING GROWTH AND SURVIVAL	RESPONSES TO GAP CREATION	SEED INTRODUCTION	SEEDLING INTRODUCTION	STAND INVENTORY	HERBICIDE	MATRICIDE	SEED INPUTS	SOIL SEED STORAGE
Mature Ecosystems																
Hammock	1	x	x							x	x				x	x
Glade (seasonally wet praire)	2	x	x							x	x				x	x
Pineland	3	x	x			x				x	x				x	x
Successional Vegetation >8 years old																
Old schinus forest no. 1	4	x	x	x		x	x	x	x	x	x	x		x	x	x
Old schinus forest no. 2	5	x	x				x	x	x		x	x				x
Myrica-schinus woodland	6	x	x	x	x		x	x	x	x	x	x		x	x	x
Young schinus forest	7	x	x	x			x	x	x	x	x	x		x	x	x
Old field no. 1	8												x			
Old field no. 2	9												x			
Successional Vegetation >8 years old																
1973 succession	10	x	x							x	x				x	x
1975 succession																
Transect	11	x	x							x	x	x			x	x
Schinus colony	12			x												
Hilsenbeck 1	13									x					x	x
Hilsenbeck 2	14									x					x	x
Hilsenbeck 3	15									x					x	x
Hilsenbeck 4	16									x					x	x
Hilsenbeck 5	17									x					x	x
Hilsenbeck 6	18									x					x	x
Hilsenbeck 7	19									x					x	x
Hilsenbeck 8	20									x					x	x
Schinus control area	21	x					x	x								x
Bulldozed area no. 1 1978	22					x				x	x					
Bulldozed area no. 2 1979	23					x	x									

Mature Ecosystem Sites

The study sites included 2 ecosystems that were never farmed (hammock and pineland), and one ecosystem (a glade) that had been farmed before 1950, but which had not been rock plowed and which contained vegetation typical of the pre-farming condition. The glade, therefore, was considered to represent mature vegetation typical of one set of site conditions, just as the hammock and pinelands were also considered to be mature communities.

The hammock (no. 1 on Fig. 2) was typical of the broadleaved, evergreen forests that are common in South Florida. This vegetation type, dominated by trees of West Indian origin, has been studied by many ecologists, including Philipps (1940), Alexander (1958, 1967), Craighead (1974), Hilsenbeck (1976a), and Olmsted et al. (1980). The forest studied is called Palma Vista Hammock, and is adjacent to the northeast corner of the study area. It had a closed canopy at 16 m, and on a 0.1 ha transect there were 11 tree species and 268 individuals ≥5 cm DBH, having a total basal area of 3.5 m^2. The soil was a >20 cm deep layer of organic matter overlying oolitic limestone that was pockmarked with solution holes. This site never flooded.

The pineland (no. 3 on Fig. 2), located <1 km north of the Park's Research Center, consisted of an open overstory of young (<50 yr) pine (Pinus elliottii var. densa) and an understory of shrubs and herbs. Such pinelands are fire maintained, and contain 17 endemic plant species (Avery and Loope 1980a). The recent fire history of the pineland study site consisted of one prescribed burn in January, 1975 and a second in November, 1979, while the field studies were in progress. The land surface is exposed limestone that has differential rates of solution, forming jagged pinnacle rock. The pineland never flooded, except where water accumulated in exposed solution pits. Soil is sparse, and consists of weathered limestone and organic debris that accumulate in solution pockets.

The glade (no. 2 on Fig. 2) was the wettest of the mature ecosystems studied, and representative of the greatest area of pre-farming vegetation in the study area. The glade selected for study was chosen, in part, because it was contiguous to an old schinus-dominated forest having similar hydrology. The glade was a seasonally wet prairie in which dominant plants included Muhlenbergia filipes, Spartina bakerii, and Cladium jamaicense. Fire is a normal environmental factor in this herbaceous vegetation type, and part of the study site burned in November, 1978. The soil consisted of 10-15 cm of Perrine marl overlying limestone.

Old Successional Vegetation Sites (nos. 4-9 on Fig. 2)

Six study sites were located in successional vegetation ≥8 yr old, and schinus was an important species in each of these. The older successional vegetation that develops after farm abandonment in this area was described by Alexander and Crook (1973), who were the first to stress the importance of schinus in the post-farming succession.

The vegetation structure of 3 of these sites is described in detail in a later section (SCHINUS FOREST STRUCTURE). The exact ages of the vegetation at these study sites is unknown, but a student at Florida Atlantic University is doing a thesis involving reconstruction of the time of release of farmland in the study region (P. Krauss, in prep.).

One of the older schinus-dominated forests (no. 1) is bordered on the north by successional vegetation dating from 1975, and on the west by the mature-glade study site. This schinus forest is quite heterogeneous, and consists of many small agricultural plots that were abandoned at different times, mostly during the 1950's. It is a wet site, and occupies former glade that had been rock plowed. In most places schinus formed a dense canopy at 8 m. The understory had little foliage, but was nearly impenetrable because of the tangle of dead, but not self-pruned, branches of schinus. This was one of the most intensively studied sites.

A second, old schinus-dominated forest (no. 2) was the only site not in or contiguous to the Hole-in-the-Donut. This forest was located adjacent to the Park airstrip, and it was included because it was the oldest, best-developed schinus forest in Everglades National Park. Its age is unknown, and rows and furrows from farming were not evident. Like schinus forest no. 1, it occupied a wet site: the wettest of any studied. The vegetation and hydrology of this site may have been influenced by the construction of the airstrip. Many of the older schinus trees fell during the 3 yr study period, perhaps indicating senescence. *Persea borbonia* and *Ilex cassine* were abundant in places.

Immediately south of the pineland site, a study area was selected in an area of rock-plowed former pineland abandoned in the 1960's. This site was called the *Myrica*-schinus woodland, and the vegetation was dominated by *Myrica cerifera* about 6 m tall plus patchily distributed schinus. The understory was conspicuously sparse, and it was this observation, plus the slow growth of naturally occurring schinus seedlings here, that inspired research conducted as part of this study which demonstrated that *Myrica* is allelopathic to schinus (Dunevitz and Ewel 1980). The soil on this site was never flooded. Gaps created by falling *Myrica* were common. Understory vegetation included shrubs typical of the adjacent pinelands (e.g. *Guettarda scabra* and *Tetrazygia bicolor*), but there was no regeneration of pine.

The fourth schinus-dominated vegetation studied was called the young schinus forest, and it was located <1 km WSW of the Research Center. It was a dense stand of nearly pure schinus, and was probably last farmed in the mid to late 1960's. The number of schinus stems per unit area and rates of schinus growth were higher here than at any other site. The site was dry, but did flood on occasion. It probably occupied land that had been a tongue of pineland extending into glade vegetation. The site had been rock plowed and farmed, and rows and furrows were still evident. Parts of the site contained vegetation that looked younger than the rest, and may have been disturbed during construction of a nearby road and military installation.

The other 2 sites occupied by successional vegetation that was >8 yr old were used only for herbicide tests. Both were on former pineland, and both were abandoned fields containing abundant schinus bushes, 1 to 5 m tall. These sites were selected because they were accessible, they had a high density of schinus bushes, and their soil surface did not flood, thus reducing the possibility of introducing herbicides into surface waters. One site was located west of the Myrica-schinus woodland and the other was east of the Scout Camp.

Young Successional Vegetation Sites (nos. 10-23 on Fig. 2)

Successional vegetation <8 yr old occupied 14 of the 23 study sites. The young successional vegetation that follows farming in the study region was described by Egler (1952), Robertson (1953), Alexander and Crook (1973), Hilsenbeck (1976b), and Loope and Dunevitz (1981b). Immediately after release from farming the soil is covered by a dense growth of forbs and grasses. Hilsenbeck (1976b) found that many of these earliest colonizers arise from seeds contained in fertilizer applied to the row crops, even though the fertilizer is presumably sterilized before it is applied. Within a year or two, 2 species become especially conspicuous: *Ludwigia octovalvis* and *Baccharis halimifolia*.

One study site was released from farming in 1973. It was a 2 ha block that was excluded from the vegetation chopping and soil disking treatment applied to most recently released farmland in the study area in 1975. This was done to retain a slightly older example of successional vegetation that might be used to anticipate by 2 yr the changes that could be expected in the successional vegetation dating from 1975. *Baccharis* was especially conspicuous at this site, but *Ludwigia* and grasses were also abundant. By 1980 the vegetation was about 3 to 4 m tall, and contained numerous schinus bushes. This site, occupying former glade, had been rock plowed and experienced wet-season flooding.

Of the 14 sites occupied by successional vegetation <8 yr old, 10 resulted from the chopping and disking that were done in late 1975. One of these was a 200 m transect extending north-south, just north of old schinus forest no. 1. This transect occupied former glade and was seasonally flooded. Near its southern end this transect experienced large amounts of flooding, perhaps because it was near an east-west road that may have impounded surface water that was slowly flowing southward.

Just west of the 1975 succession transect was an area of about 10 ha that had been invaded by schinus very early after the chopping and disking of 1975. This colony of schinus was visible from the air by 1977, and in 1978 was selected as one of the areas where schinus phenology was monitored on 100 trees. These were the youngest schinus trees whose phenology was observed, and by 1980 most were reproductively active.

The other 8 study sites containing vegetation dating from 1975 were the control treatments located within study plots established in 1975, and named in Table 1 "Hilsenbeck", after the investigator who designed the study. The exact location of these study plots, their early vegetation, and their soils are described in Hilsenbeck (1976b). Four of the

Hilsenbeck plots (nos. 1 through 4) are on Rockdale loam soil that prior to farming was occupied by pineland and short-hydroperiod prairie. The other 4 are on Perrine marl that prior to farming was occupied by sawgrass glade and seasonally wet prairie, although plot 8 may include some Rockdale soil. The plots, ranked from driest to wettest based on the depth and duration of flooding, were 1, 2, 3, 4, 8, 7, 6, 5. The Hilsenbeck plots were used primarily for studies of schinus seed introduction, soil seed storage, and seed inputs. Just northwest of the young schinus forest site was a similar area, also on former pineland, where schinus control was attempted in 1978 (Breen 1978). Some schinus trees were pulled up, others were bulldozed, and others were felled. Some of the stumps were treated with herbicides. This disturbed area was the youngest vegetation available when field research started in 1978, and was chosen to evaluate the ability of schinus to invade disturbed habitats. Studies conducted there included schinus seedling dynamics, schinus seedling growth and survival, and soil seed storage. Following the attempted schinus control, schinus quickly re-dominated the vegetation on this site.

The northwest corner of old schinus forest no. 1, at its point of intersection with the mature glade, was the site of a 1 ha schinus-control operation in 1978. The vegetation was bulldozed, piled, and burned. Immediately thereafter plots were established to monitor revegetation by species from the contiguous glade and schinus forest. This site was also used for test plantings of schinus seedlings and for schinus seed introduction studies.

In 1979 the vegetation on a large area (>50 ha) occupied by vigorous, young schinus forest located southeast of the Research Center was bulldozed, windrowed, and burned. The site included former pineland at its northern end and former glade at its southern end. This site, like other areas of attempted schinus control, was used to monitor schinus dispersal and reinvasion. The early succession on this site is described in Loope and Dunevitz (1981b).

HYDROLOGY

Methods

Water is the environmental factor that changes most during the seasons in South Florida, and strongly influences all vegetation, including schinus. Thus, water-table depth and surface flooding were monitored on several study sites.

Depth of the water table was measured from staff gauges installed in natural sinkholes, in shallow soil pits excavated to the limestone bedrock, or in irrigation wells remaining from the time the area was farmed. These gauges extended to different depths (19 to >176 cm), depending upon the type of "well" available. The water depth at each site was recorded approximately every 20 days.

Because of natural microtopography and the rows and furrows made by farmers, the soil surface was not perfectly flat at any site. Thus, the depth of the water table told only part of the story concerning differences in soil water among sites. Therefore, the amount of soil surface that was covered by floodwaters was also recorded at 9 sites. At each site 100 wire stakes were placed at randomly selected points along a 200 m transect. The number of stakes occupying microsites where the surface was flooded was recorded each time the water table depth was measured.

Results

Considering the vagaries of South Florida rainfall, seasonal fluctuations in water-table depth were remarkably consistent on all 9 sites from June, 1978 through October, 1980 (Fig. 3). The hammock, where the water table seldom got closer than 40 cm to the surface, was the driest site. The pineland and Myrica-schinus woodland (occupying former pineland) were also on dry sites, and the water table there was usually >20 cm below the soil surface.

The deepest well monitored throughout the study period was in the Myrica-schinus woodland, and in April, 1979 the water table on that site was 1.7 m below the surface. On 24 April, 1979 the study area was hit by an unprecedented dry-season rainstorm that dropped >23 cm of rain in 24 hours. Within 2 days the water table in the Myrica-schinus woodland rose >1.5 m, and soon thereafter reached its 1979 peak when it came within 12 cm of the soil surface.

A deep well was not monitored in the young schinus forest until after May, 1979, but in April, 1980 the water table at that site was 110 cm below the surface. On the same date the water table was 135 cm below the surface in the Myrica-schinus woodland. Thus, the young schinus forest occupies a site that is not much wetter than the Myrica-schinus woodland, which is known to be former pineland.

In the glade, old schinus forests, and young successional vegetations, the water table was usually within 30 cm of the surface throughout the wet season (June to October), but changes in water-table depth of 20 cm or more within a month were not uncommon.

On 2 sites--the hammock and the Myrica-schinus woodland (occupying rock-plowed pineland)--the soil surface was never flooded. The pineland had some surface water in shallow solution pits on 5 of 32 observations, but these covered only 1 to 2% of the surface. The other 6 sites, occupying glades or former glades, experienced varying degrees of surface flooding (Fig. 4). Surface flooding extended from June through October, and was greatest late in the rainy season, usually peaking in September. On some sites 80% of the soil surface was flooded at times, but such extensive flooding never occurred for continuous periods longer than 2 months. No site was flooded in November through May, except after the unusually heavy rainstorm of late April, 1979.

Although schinus seedlings are flood tolerant, rapid changes in water depth were frequently correlated with schinus seedling mortality. Rapid increases in water depth drowned some seedlings, while rapid drops in the water table often increased mortality due to drought. The response of native species to rapid oscillations in water-table depth are not

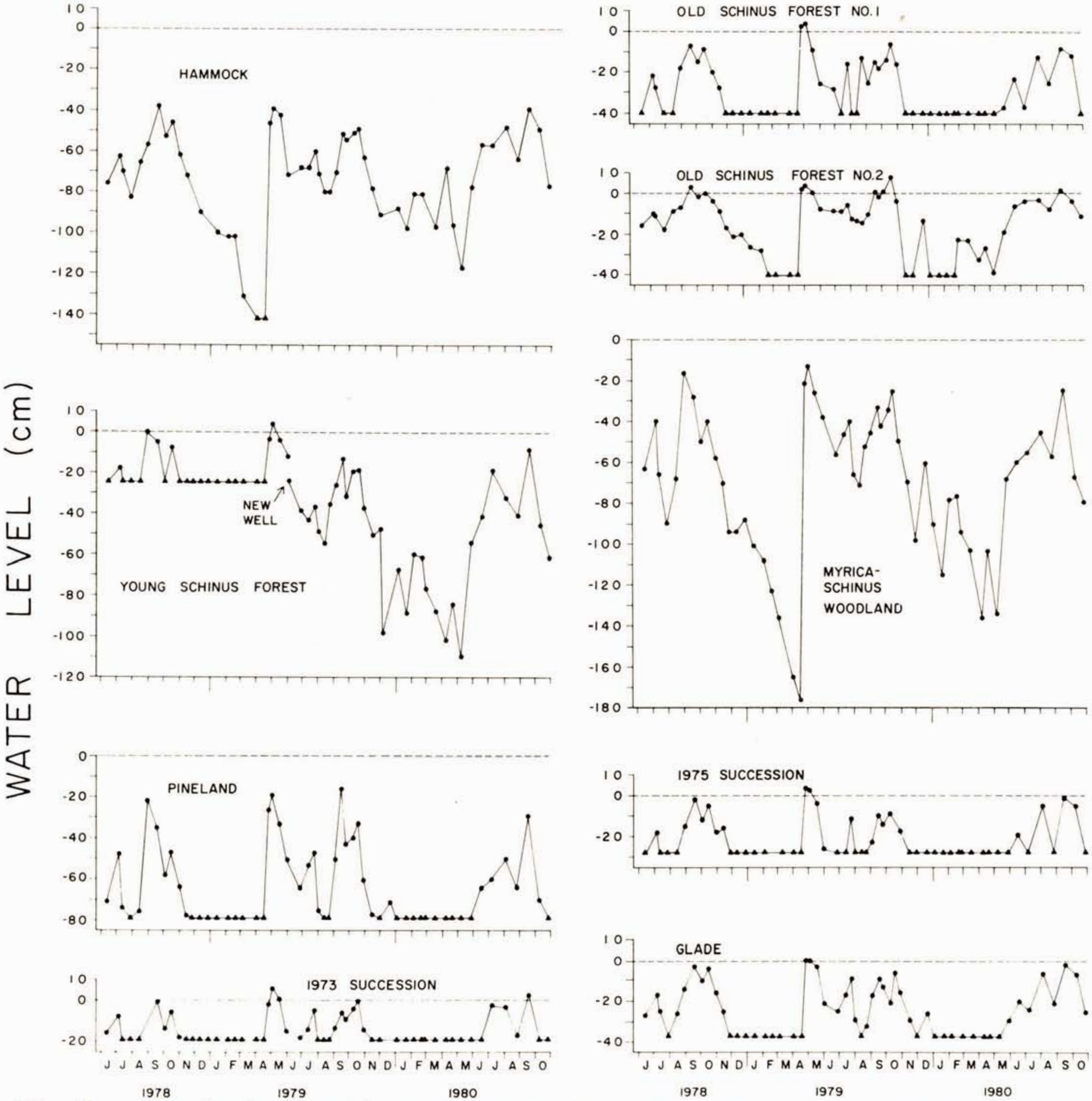


Fig. 3. Water depths in wells at the study sites. Triangles indicate well bottoms.

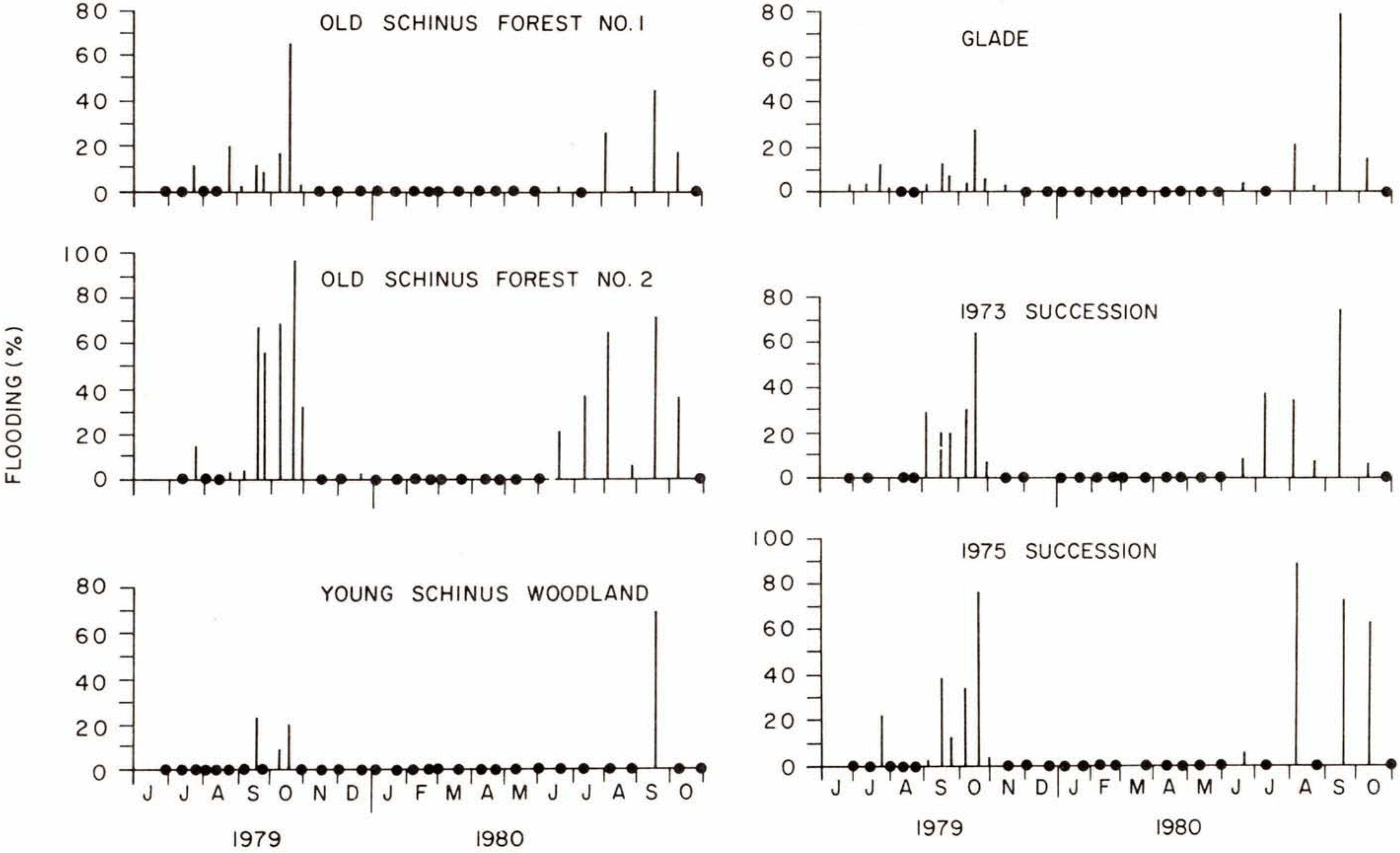


Fig. 4. Surface flooding on 6 study sites. Each observation was based on 100 sample points.

known, but some species, such as Ludwigia spp. and sawgrass (Cladium jamaicense), seem to be at least as well adapted to changing water levels as is schinus. Thus, water levels might be one important environmental factor that could be manipulated to influence schinus and the competing native vegetation.

PHENOLOGY

Methods

In October, 1978 we initiated a phenological study of 400 schinus trees: 100 in each of 4 sites. The 4 sites were: 1) the roadside fringe of the old, schinus-dominated forest along the Hayes Barn road, 2) roadside trees near the edges of the Myrica-schinus woodland, including some along the boundary between that woodland and the pineland, 3) the young schinus-dominated woodland east of the northern-most missile base, and 4) a colony of young schinus bushes that were among the first to invade former farmlands that had been disked in late 1975.

Each tree was permanently tagged, and all observations were made on a tree-by-tree basis. Observations were usually made biweekly, but some intervals between observations were as long as one month. During periods of intense reproductive activity observations were made weekly.

At the time of each observation, each tree was scored with respect to the following 3 features:

LEAF FLUSHING ACTIVITY (1 and 3 not mutually exclusive)

1. Leaf drop
2. No leaf activity
3. New (red) leaves present

FLOWERING ACTIVITY

1. No flowers present
2. Flowers present, mostly closed
3. Flowers present, mostly open

FRUITING ACTIVITY

1. No fruits present
2. Fruits present, mostly unripe (green)
3. Fruits present, mostly ripe (red)

Schinus is dioecious, i.e. it has trees with only female flowers and trees with only male flowers. The sex of each tree was recorded the first time it flowered.

Results

Leaves

Schinus is an evergreen tree, and produces leaves almost continuously throughout the year. The leaf drop data (Fig. 5) may reflect some of the observer-dependent subjectiveness involved in evaluating leaf phenology. The first 6 mo of data, when little leaf drop was recorded, were taken by 1 observer, whereas the later data were taken by 2 others. Leaf drop is nearly continuous, but was lowest on all sites during November through February. Also, there were differences among sites. The schinus trees on 2 of the sites--the Myrica-schinus woodland and the young schinus forest--had reduced leaf drop during the wet months, whereas trees on the other 2 sites did not show wet-season decreases in leaf drop.

Leaf flushing, or the production of new leaves, is easier to evaluate than is leaf drop. Schinus, like many tropical trees, flushes nearly continuously, except during October and November when reproductive activity is at its peak (Fig. 6). Schinus trees on each of the 4 sites exhibited similar patterns of leaf flushing, except that those in the young schinus forest flushed less continuously than those on the other 3 sites. After flowering, male trees resumed flushing more rapidly than did female trees. This may reflect the added energetic cost of fruit development incurred by the females.

Reproduction

Five of the 400 trees selected for phenology observations never flowered, so their sex was not determined. All of the trees observed were old enough and large enough to flower, so the 5 that did not may represent a small fraction (about 1%) of the population that does not reproduce. Of the 395 that did flower, 196 (49.6%) were males and 199 (50.4%) were females. Thus, the schinus population is almost exactly one-half males and one-half females.

The dioecy of schinus is not universal. Some trees that produced fruits later bore male flowers; it is not known whether the fruits arose from female flowers or from hermaphroditic flowers. Male schinus flowers possess a pistillode (rudimentary or vestigal pistil), and female schinus flowers possess staminodes (vestigal stamens). It is not uncommon for species that are dioecious to have some individuals that occasionally produce hermaphroditic flowers or flowers of each sex. In schinus, such individuals probably constitute about 1% of the population.

Schinus flowering is remarkably synchronous and compressed, and occurs at the same time year after year. Schinus' flowering activity (Fig. 7) is almost an exact inverse of its leaf flushing activity (Fig. 6). Flowering begins in September and by mid-October almost every tree is in flower. Most flowering activity ceases in early November.

A small fraction of the population (about 10%) flowers in March-May. Some of these late bloomers are trees that did not flower in October, but for most the spring reproductive activity is a second flowering

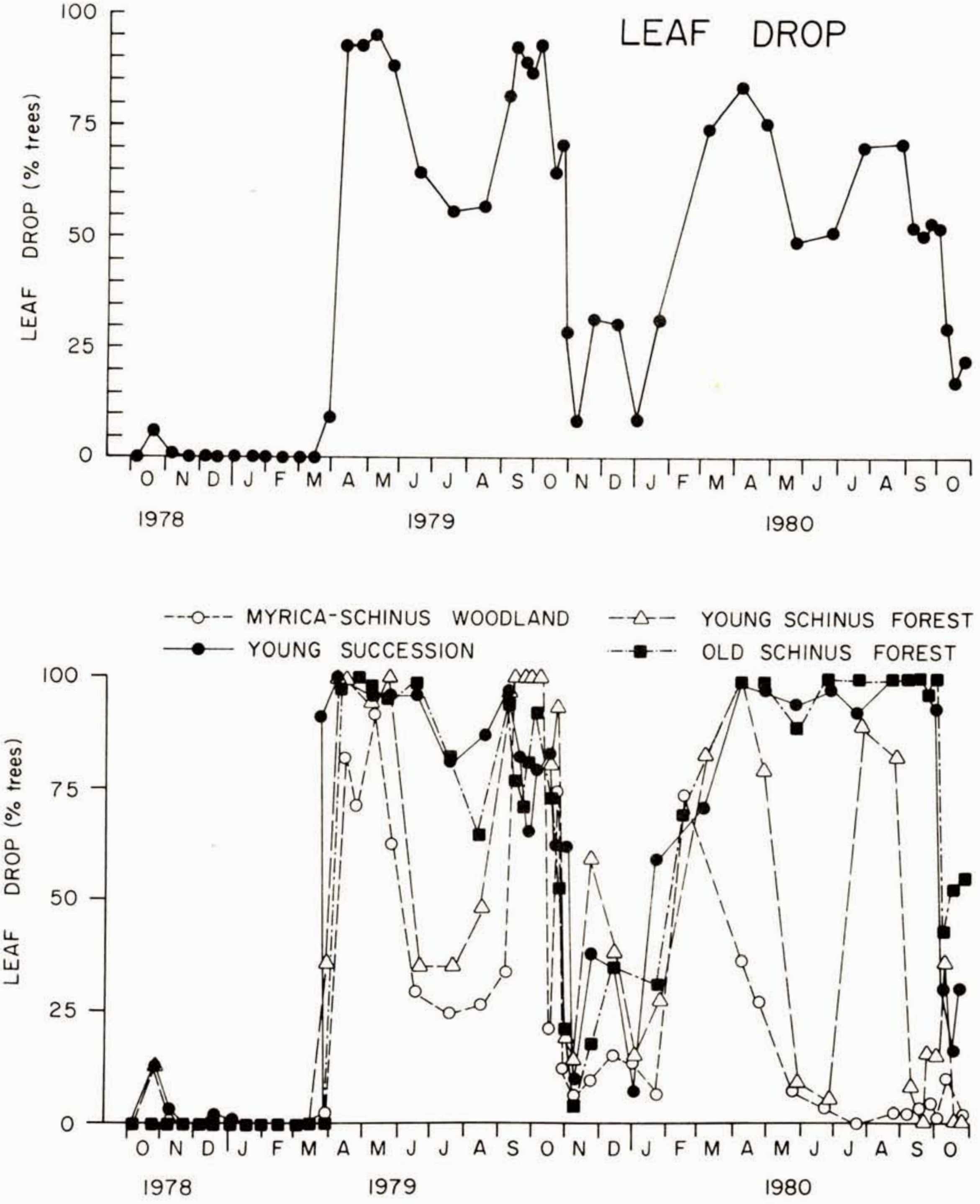


Fig. 5. Schinus leaf drop. Upper: summary curve for 4 sites combined. Lower: individual curves for 4 sites, 100 trees per site.

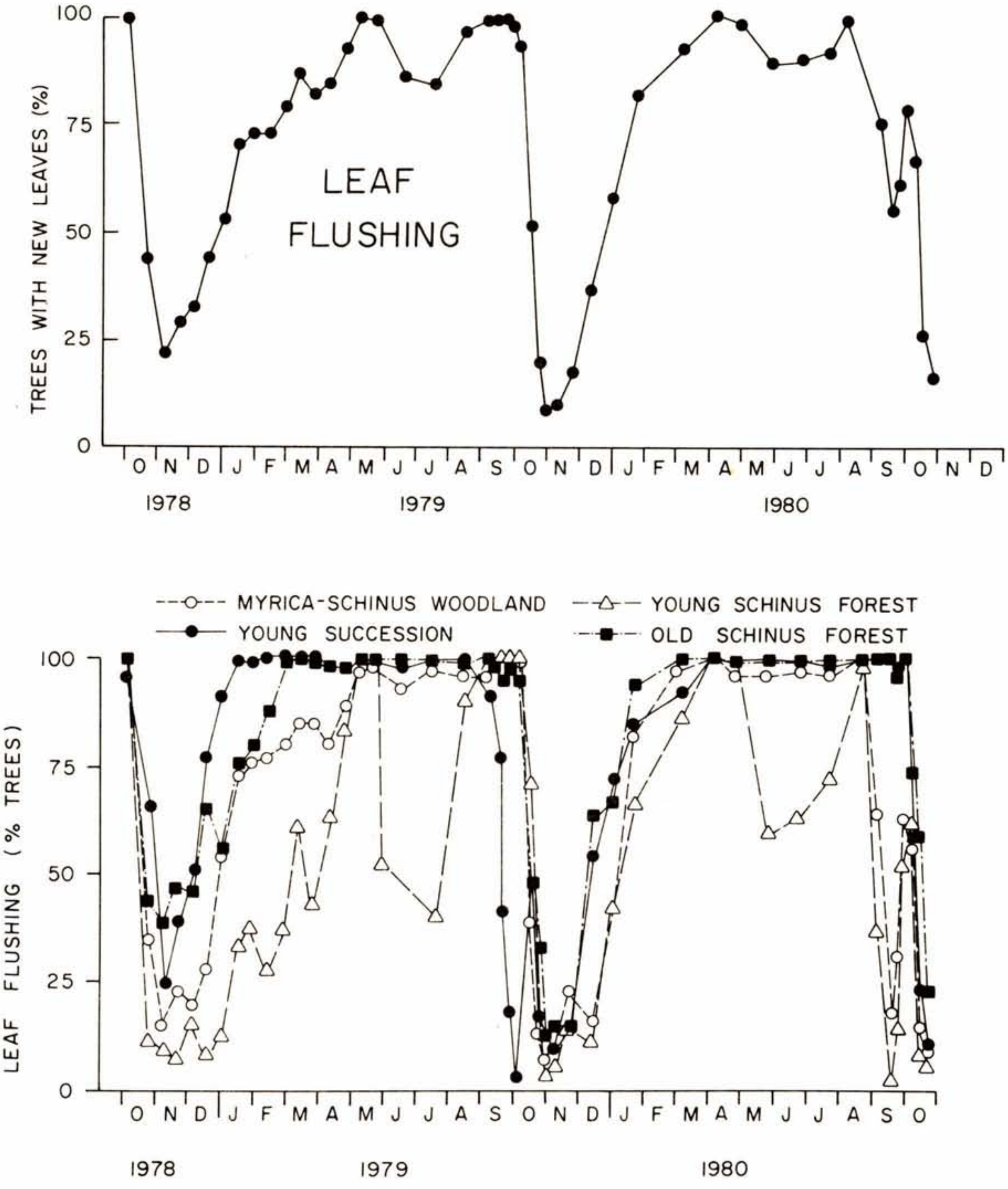
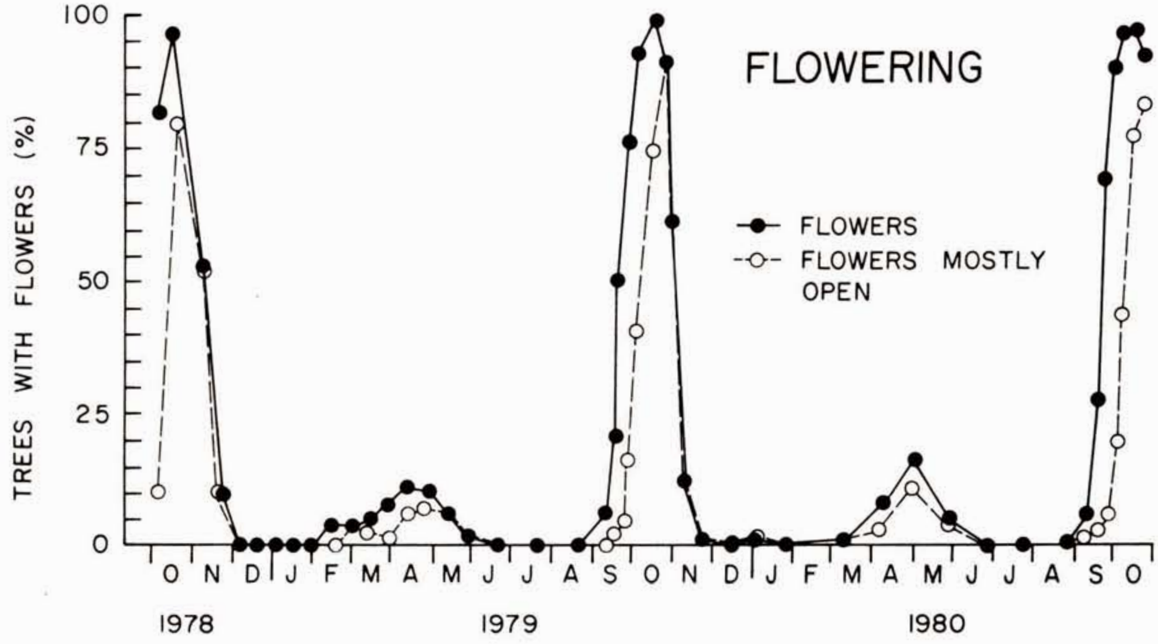


Fig. 6. Schinus leaf flushing. Upper: summary curve for 4 sites combined. Lower: individual curves for 4 sites, 100 trees per site.



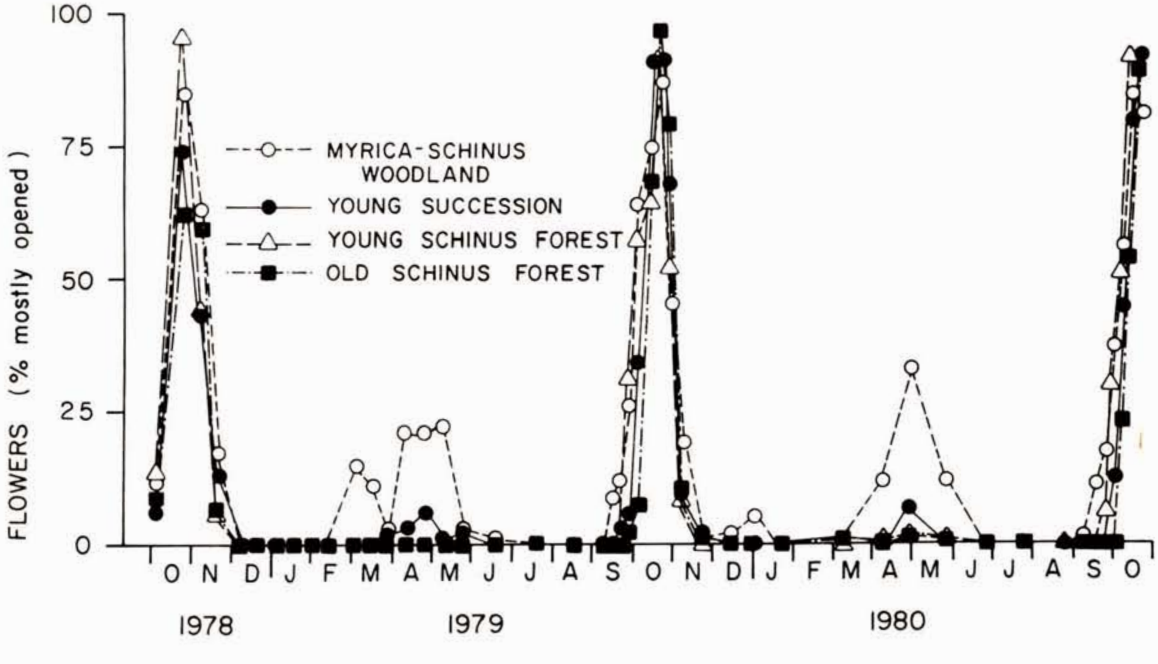


Fig. 7. Schinus flowering. Upper: summary curve for 4 sites combined. Lower: individual curves for 4 sites, 100 trees per site.

period. Spring flowering was more common in the Myrica-schinus woodland population than at other sites (Fig. 7).

Fruit ripening follows close behind flowering, and by December almost all fruits are red (Fig. 8). Most dispersal takes place soon thereafter, but some trees still retain fruit as late as July or August. Dehiscence of fruit-bearing inflorescences is faster on some sites than others. For example, fruits were retained longer in the Myrica-schinus woodland and in the young schinus forest populations than in the populations at the other 2 sites (Fig. 8). These were the same 2 sites where leaf drop (Fig. 5) also lagged. On all sites dispersal is complete before the next season's reproductive activity begins.

POLLINATION

Methods

Studies of schinus pollination included work on pollen vectors, with emphasis on insect visitors and their pollen loads; studies of flower longevity and nectar secretion; and measurements of fruit set on exposed inflorescences and on those from which insects were excluded. In addition to project personnel, Robert Whelan and Kenneth Young, both of the University of Florida, made substantial contributions to the schinus pollination research.

Pollen Vectors

The first pollen-vector experiment was designed to find out whether or not schinus pollen was wind dispersed. In October 1979, flowering female schinus saplings (mean height = 1.5 m) were transplanted from the field into pots, and grown in a shadehouse for 7 days. Then, all open flowers were removed from each inflorescence and nylon bags were secured around the unopened flower buds to prevent pollination by insects. Pollen traps were constructed by punching 2 holes in aluminum tree tags, and placing cellophane tape on 1 side of the tags so that pollen landing on the holes would be stuck to the exposed adhesive. When the buds opened (after about 3 days), the saplings were placed, 1 at a time, in front of a floor fan (Table 2), and wind velocities were measured with a Dwyer Instruments hand-held anemometer. A pollen trap was hung in each tree, and the fan was run for 5 min. While the fan was running, a freshly cut male inflorescence was shaken gently in front of it. A control for the seed set estimated was conducted by hand pollinating the flowers on 1 sapling. Treated females were rebagged and returned to the shadehouse, and the fruits on each were counted after 45 days. In addition, 1 pollen trap was placed on a table, and a male inflorescence was shaken vigorously over it. All pollen traps were examined under 100X magnification.

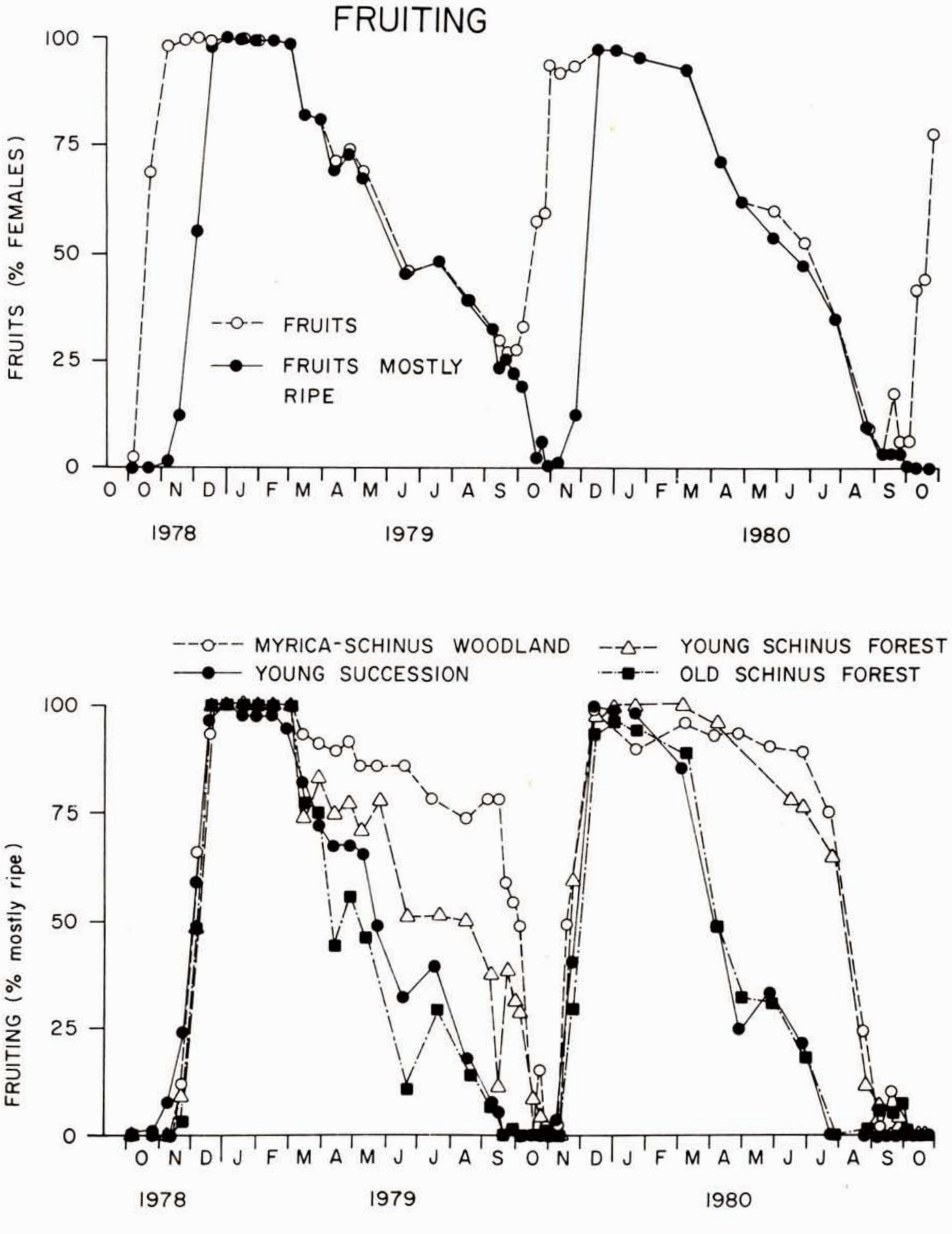


Fig. 8. Schinus fruiting. Upper: summary curve for 4 sites combined. Lower: individual curves for 4 sites, 100 trees per site.

Table 2. Treatments to test wind movement of schinus pollen.

Distance from fan (m)	Wind Velocity (km/h)	No. of Samplings	Inflorescence Bag
0.5	13	2	Not Removed
0.5	13	1	Removed
1.0	8	1	Removed
2.0	5	1	Removed

Insect visitors to schinus were collected during the 1979, 1980, and 1981 flowering seasons. All collections were made within 1 km of the Research Center. The 1979 and 1980 collections were lost, but species collected in 1981 were identified. The 1979 collection was opportunistic, and contained <40 specimens; the other 2 collections were done more systematically.

In 1980, collections were made October 14-18, but only those insects caught on the 15th (a warm, sunny day) were used to calculate the timing of insect visiting, the relative abundance of species of visitors, and pollen loads. Most collecting was done between 0700 and 1900, as insects were rare before and after this period. However, frequent observations were made earlier and late at night to verify that there were no nocturnal visitors. Insects were caught with long-handled sweep nets, and 3 people netted simultaneously throughout the day. Collecting was concentrated at female trees because insects carrying pollen at female flowers represent the potential input of pollen to the tree rather than the pollen load just collected by the insect, as would be the case for insects collected around male flowers. Each insect was placed in a vial and labelled with the time of collection. These specimens were later killed by freezing and placed in a preservative solution (5% glycerine in 70% alcohol). Only legs and proboscises of lepidoptera were preserved. In the laboratory, the vial containing each insect in preservative was shaken for 24 h on an orbital shaker. The insect was then removed for identification and the preservative solution was centrifuged at 1000 rpm for 15 min. The pellet at the bottom of the centrifuge tube was removed with a teat pipette and transferred to a microscope slide for identification of schinus pollen grains (Fig. 9).

In 1981 schinus insect visitors were studied at hourly intervals, from 0700 until 1800, on October 8. In each interval, a female tree was observed for 15 min and a male tree was observed for 15 min. Observations included the identity and estimated relative abundance of all insect visitors. The remaining portion of each interval was devoted to capture of insects from schinus flowers. Time of capture and tree sex were recorded, and specimens were preserved in alcohol. Observations and insect capture were done from the roof of a vehicle to give access to the upper branches of roadside trees. In the laboratory the insects in alcohol were sonified to remove pollen, and the complete pollen load

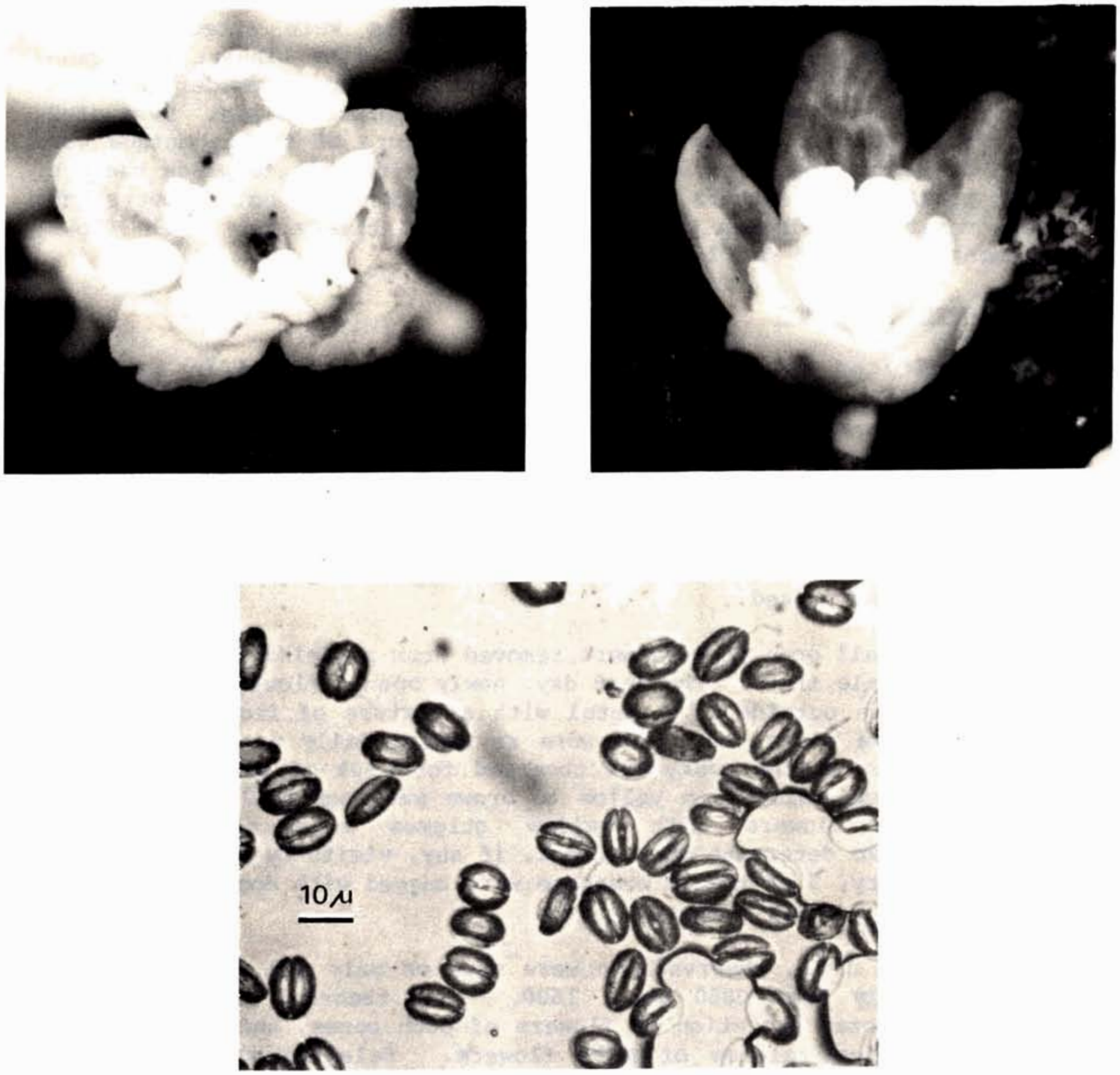


Fig. 9. Schinus flowers and pollen. Upper left: male flower. Upper right: female flower. Note pistillode in male flower and staminodes in female flower. Flowers are 2-3 mm in diameter.

from each specimen was mounted on a microscope slide for counting and identification.

In 1980 and 1981, pollen-tracking experiments were attempted, but failed. The technique, similar to that described by Linhart and Feinsinger (1980), involved marking flowers with fluorescent powder having a grain size only slightly larger than that of schinus pollen. Dyes of 2 colors were tested: orange and yellow. Failure of the technique was due to the tiny flowers of schinus, making it difficult to place the dye powder precisely on anthers, and the great abundance of both flowers and insect visitors, diluting the dye powder to relatively few female flowers among a "sea" of millions.

Flower Responses

The longevity of male and female flowers was determined in 1980 and 1981. In 1980, all opened flowers were removed from 20 panicles distributed among several female trees and 20 panicles distributed among several male trees. Branches supporting the panicles under study were bagged, then revisited at 0800 the next day, when newly opened flowers were marked with fluorescent dye. Panicles were revisited at 1100, 1400, and 1700 of that day, and at 0800 the following morning. Bags were only removed briefly during each visit, when newly opened flowers were counted and marked.

Also in 1980, all open flowers were removed from panicles on 10 branches of several female trees. The next day, newly opened flowers were marked by painting the outside of 1 petal with a mixture of fluorescent dye, water and white paste. Flowers were revisited daily until dehiscence and/or swelling of the ovary was observed for >90% of the flowers. A change in stigma color from yellow to brown was soon followed by ovary swelling, so flowers with yellow stigmas were classified as "receptive". To determine what effect, if any, visits by insects had on flower longevity, 5 of the 10 branches were bagged with double-thickness bridal mesh to exclude insects.

On October 10, 1981, observations were made on male and female flowers at least hourly from 0800 until 1600. Data recorded included petal opening and nectar secretion of flowers of both sexes, and stamen positions and pollen release of male flowers. Selected specimens were preserved in alcohol so that field observations could later be corroborated in the laboratory with the aid of a microscope. Measurements of nectar quantity and sugar concentration, and flower longevity, were made from October 7 to 11 on bagged and unbagged inflorescences. Nectar was measured to the nearest 0.03 μl using a 1 μl capillary tube, and sugar concentrations were measured to the nearest 1% using a refractometer.

Fruit Set

In 1979, 2 large, flower-bearing female schinus trees growing along a field edge were selected, and all open flowers were removed from 2 inflorescences on each tree. On each tree, 1 inflorescence was bagged with a nylon sack and the other was left exposed. The number of fruits that formed on each of the 4 inflorescences was later counted.

This 1979 pilot experiment produced interesting results, so the methodology was improved and the experiment run again in 1980. Bagging experiments were conducted at 3 times: early in the flowering season, at mid-season (when flowering activity peaked), and late in the flowering season. Early- and late-season samples consisted of 5 trees each; the mid-season sample consisted of 10 trees. On each tree, 4 inflorescences were chosen, and none was > 2 m above the ground. Of these, 2 were at the outside of the crown and 2 were well inside the crown. One inflorescence at each position (inside or outside of crown) was bagged and the other was left unbagged. For the mid- and late-season samples, some removal of open flowers was necessary, and this was done (using forceps) immediately prior to bagging. Open flowers were also removed at the same time from unbagged inflorescences. The insect-exclosure bags were constructed of 1 mm mesh bridal screen covering a wire frame 17 cm in diameter and 31 cm long. This cylinder had a 17 cm-long white cotton sleeve attached to its open end, and the entire exclosure was slipped over the branch, after which the sleeve was tightly secured. Leaves in the bag were not removed and they helped keep the cylinder from contacting the inflorescence.

When most fruits on an inflorescence were red they were harvested, except in the case of the late-season samples when maturation was unusually prolonged, and some inflorescences were harvested while they still had green fruits. Viability was tested only for seeds from the late-season samples, and was determined by placing subsamples of fruits (n = 1 to 20) on moist sand treated with a fungicide (50% captan) in a Petri dish. Germination was monitored every 1 to 3 days for approximately 30 days.

To estimate maximum potential fruit set, it was necessary to estimate the number of flowers per panicle. These were too numerous to count individually, so 52 panicles were harvested from female trees. The number of flowers on each was counted, and linear regressions were calculated using number of flowers as the dependent variable and 3 other measures as independent variables: panicle length, number of branchlets per panicle, and the ratio between panicle length and number of branchlets. None of the 3 coefficients of determination was >0.5, and the 3 did not differ greatly, so panicle length ($r^2 = 0.47$) was used to estimate flower number because it was the easiest variable to measure.

Results

Pollen Vectors

None of the pollen traps hung in schinus trees placed in front of a fan blowing across a male inflorescence captured any pollen. Only the pollen trap that was placed on a table and had a male inflorescence vigorously shaken above it trapped pollen; it also trapped entire anthers. Each of the female inflorescences that was bagged after being placed in front of the fan blowing across a male inflorescence had >20 flowers, but with the exception of 1 fruit on the plant at 0.5 m, none of them bore fruit. However, the hand-pollinated inflorescence produced only 1 fruit, but this lack of fruit set is thought to have resulted from structural damage to the flowers caused by crude technique.

Schinus pollen grains and anthers are sticky, and the pollen is not readily wind transported.

On 1 day in October, 1980, 31 species of insect visitors were netted at schinus trees (Table 3). Of these, 25 species were collected at female trees, where most collecting was done. By far the most abundant visitor was a syrphid fly, Palpada vinetorum, which accounted for 44% of the individuals caught. Although most individuals caught were dipterans, the order Hymenoptera accounted for more species (19) than any of the other 4 orders caught (Table 3). Of the 31 species caught, 13 carried schinus pollen, and some individuals (7 of 16 schinus-pollen-bearing individuals of Palpada vinetorum and 1 of 3 Urbanus proteus) carried schinus pollen exclusively.

The activity times of the 5 most abundant insect visitors overlapped considerably, and each was active for at least 4 hr; the syrphid was active all day (Fig. 10). Insect activity of all species combined was steady throughout the day, reaching a peak between 1500 and 1600, then decreasing rapidly toward dusk (Fig. 11). There was no insect activity before 0800 or after 1800.

The 1981 collection of insect visitors is described in Table 4. Male schinus flowers attract many insect species that forage on nectar, or pollen, or both. Most insects that forage on male schinus flowers later than about 1000 pick up some pollen grains. Some of these were found later to be foraging on female flowers, and thus were potential pollinators. These included the most abundant visitor--Palpada vinetorum--plus honey bees (Apis mellifera) and 2 wasps (Polistes sp. and Mischocyttarus cubensis). Some pollen-laden insects were observed only on male flowers, and may be pollen thieves. Female flowers produce only nectar, which is presumably the resource sought by most foragers on female flowers. However, male and female schinus flowers look remarkably similar in both color and pattern, and the pollen is almost identical in color and placement with the nectary ring on the female flower. K. Young (pers. comm.) suggests that female flowers may be male flower mimics which attract foragers that might be after pollen, a phenomenon reported for the Caricaceae (Baker 1976).

Flower Responses

The 1980 data demonstrated that both male and female schinus flowers open early in the day, and that male flowers last only 1 day, whereas female flowers last longer (Table 5). Abscission of male flowers was independent of whether or not they were visited by insects. These observations were corroborated by 1981 observations.

Table 3. Insects caught at schinus, and their pollen-bearing status, Oct. 1980

	Total caught	Caught at female schinus	
		Number caught	Number with schinus pollen
DIPTERA			
Palpada vinetorum	62	42	16
Fly 2	1	1	0
Fly 3	8	6	1
Fly 4	1	1	0
Fly 5	2	2	0
Fly 6	1	1	0
HYMENOPTERA			
Apis mellifera	10	6	4
Bee 1	5	3	1
Bee 3	2	0	-
Bee 4	2	2	1
Bee 5	2	1	1
Wasp 1	3	2	1
Wasp 2	2	2	1
Wasp 3	4	4	0
Wasp 4	2	2	0
Wasp 5	6	6	2
Wasp 6	1	1	1
Wasp 7	1	0	-
Wasp 8	1	1	0
Wasp 9	3	3	2
Wasp 10	2	0	-
Wasp 11	4	4	1
Wasp 12	1	1	0
Wasp 13	1	1	0
Wasp 14	2	1	0
LEPIDOPTERA			
Urbanus proteus	11	7	3
Heliconius charitonius	1	0	-
Agraulis vanillae	1	1	0
Anartia jatrophae	1	0	-
HEMIPTERA			
Hemiptera 1	1	1	0
COLEOPTERA			
Coleoptera 1	1	0	-
TOTAL	145	102	35

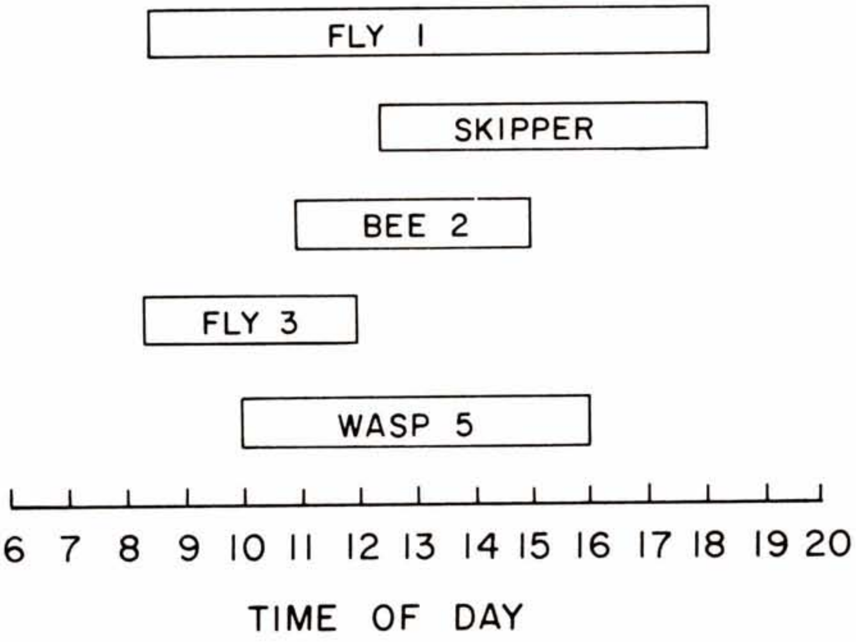


Fig. 10. Activity patterns of 5 abundant insect visitors to female schinus trees. Fly 1 was a syrphid, Palpada vinetorum, likely to be the most important schinus pollinator. All observations were made in October, 1980.

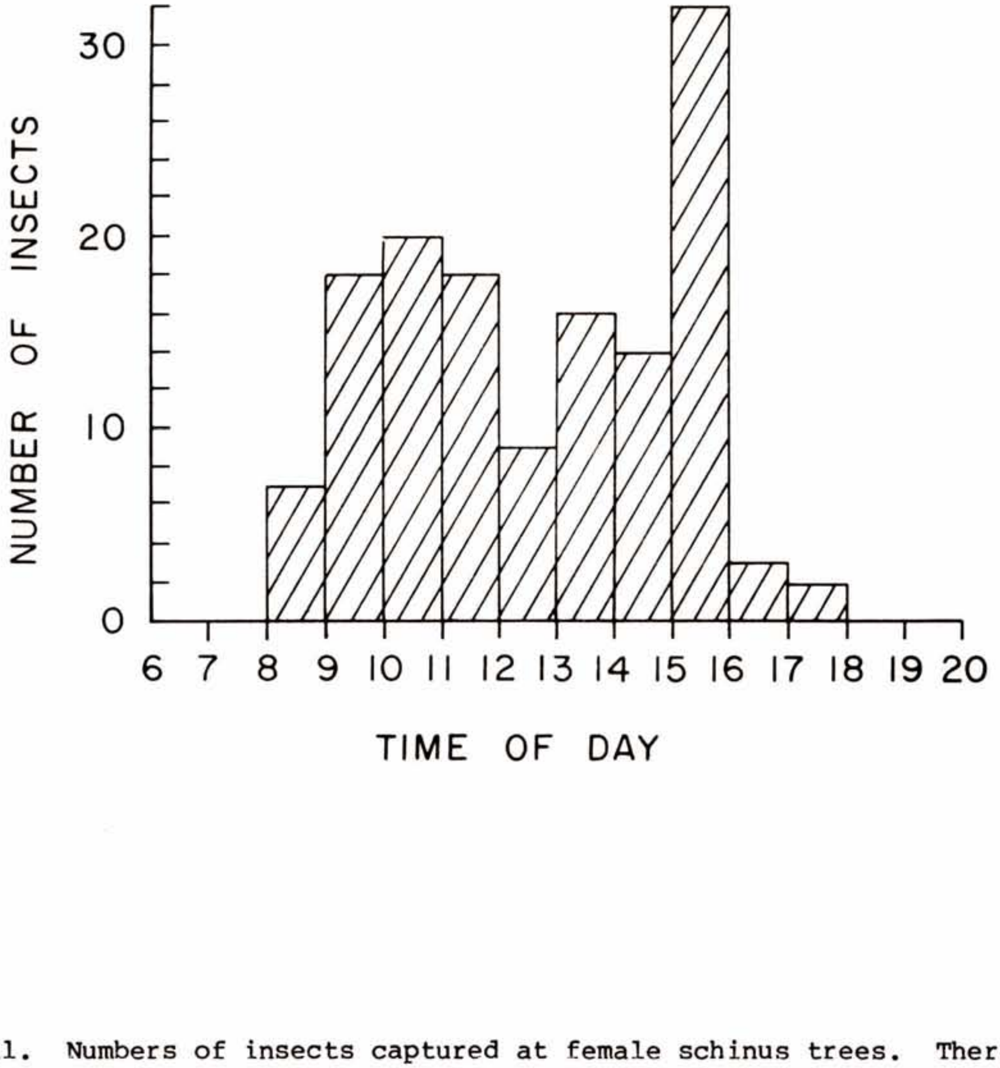


Fig. 11. Numbers of insects captured at female schinus trees. There were no nocturnal visitors. All observations were made in October, 1980.

Table 4. Insect visitors to female and male schinus flowers 7-10 October 1981. Asterisk indicates that captured individual carried schinus pollen.

Species	Sex of tree where captured	
Cantharidae		
Chauliognathus pennsylvanicus		M*
Lycaenidae		
Strymon cecrops		M
Nymphalidae		
nymphalid sp.		M
Heliconiidae		
Heliconius charitonius		M
Hesperiidae		
Urbanus proteus		M*
hesperiid sp. #1	F	M
hesperiid sp. #2	F	M
Ctenuchidae		
Compstonia sp.		M*
Bibionidae		
Plecia nearctica	F	M*
Syrphidae		
Palpada vinetorum	F*	M*
Palpada albifrons		M
Ocyptamus fuscipennis	F	M
Baccha clavata		M*
Toxomerus floralis	F	
Meromacrus acutus		M*
Calliphoridae		
Cochliomyia macellaria	F	M
Formicidae		
Pseudomyrmex mexicana	F	M*
formicid sp.	F	
Vespidae		
Polistes sp.	F*	
Mischocyttarus cubensis	F*	M
Euodynerus sp.	F	
Pompilidae		
Anoplius sp.		M*
Sphecidae		
Ammophila sp.		M*
Halictidae		
Augochloropsis sp.	F	M*
Anthophoridae		
Xylocopa sp.		M*
Apidae		
Apis mellifera	F*	M*
Dipteran sp.	F	
Hymenopteran sp. #1	F	
Hymenopteran sp. #2	F	

Table 5. Time of opening of female and male schinus flowers. Values are number of new flowers on 20 panicles at each sample time.

	Day 1				Day 2	Flowers opened by 0800 day 1 and still present 0800 day 2
	0800	1100	1400	1730	0800	(%)
Female	58	0	0	0	77	95
Male	85	14	0	2	49	0

The observation that female flowers lasted >1 day led to experiments designed to measure their longevity, and to determine the impact of insect visits on that longevity. Most female flowers had receptive stigmas for 2 days after opening, but only about half had receptive stigmas when they were 4 days old, and almost none had receptive stigmas by day 6 (Fig. 12).

Data from October, 1981 on nectar volumes and sugar concentrations of bagged and unbagged flowers of both sexes are summarized in Table 6. Sucrose concentrations in the nectar of flowers of both sexes is about 44%, but females produce about 4 times more nectar than do male flowers. The tendency may be for foragers to make more visits per flower to female flowers than to male flowers. This would increase the probability of pollen deposition on stigmas. Nectar volumes of female flowers open to insect visits were only about 25% of those in flowers protected by insect exclosures. Apparently some individual male trees do not secrete nectar. One bagged male inflorescence never had nectar over the course of several days.

Table 6. Nectar volumes and sucrose concentrations of schinus flowers. Each value is a mean of 25 to 90 flowers.

Flower sex	Exposure	Mean nectar volume (μl per flower)	Mean sucrose concentration (%)
Female	Unbagged	0.008	44
	Bagged	0.036	42
Male	Unbagged	0.009	45
	Bagged	0.008	43

Male flowers are slightly open at dawn. By 0800 the petals are separated and sometimes the flowers contain a liquid that is mostly dew. Sugar concentrations in these early morning flowers were about 4%, so a very

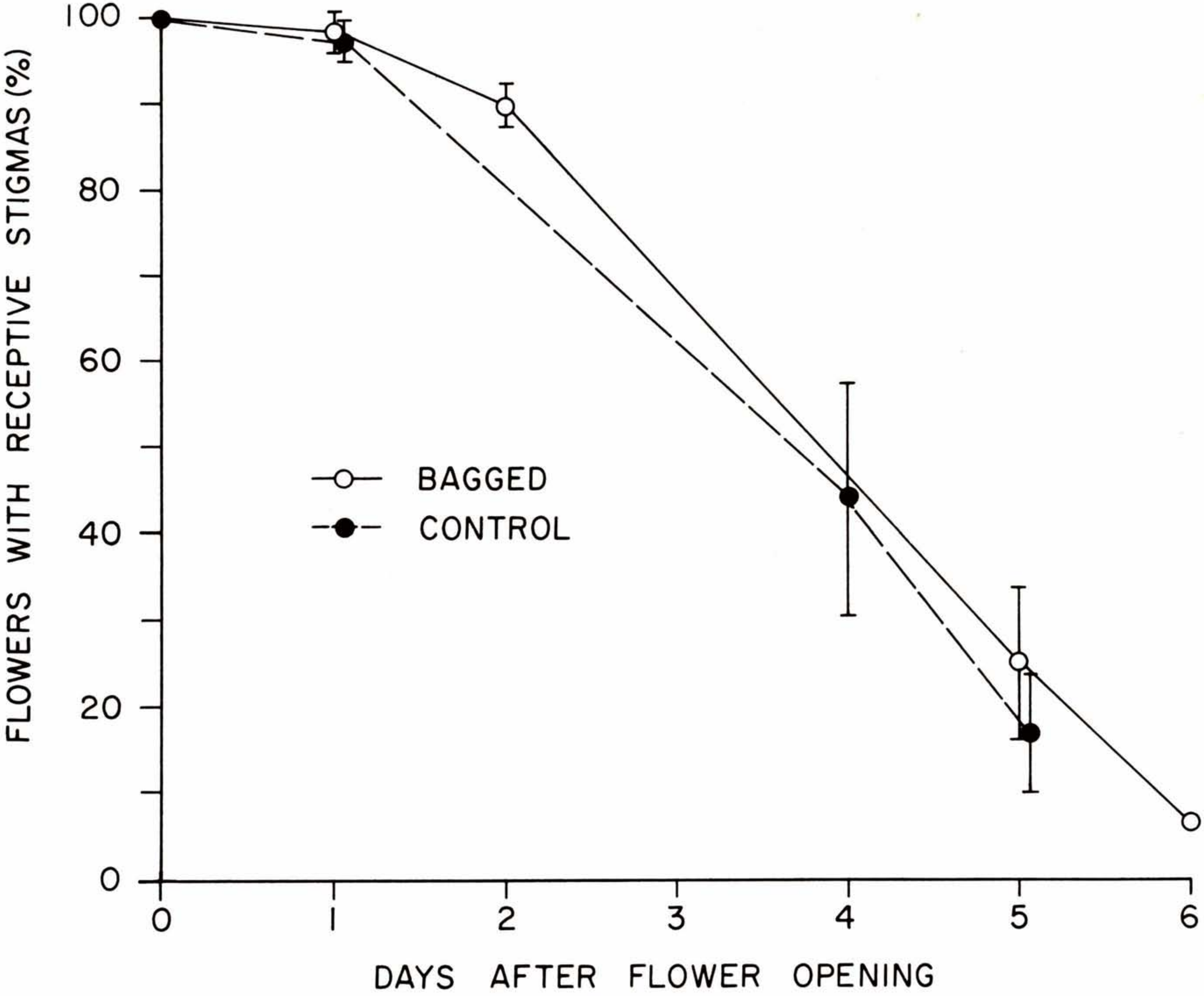


Fig. 12. Longevity of female schinus flowers. Male flowers last only 1 day.

dilute nectar is occasionally present. Butterflies (Urbanus, other hesperiids, Heliconius) and flies, (Cochliomyia macellaria and unidentified species) forage for this dew-nectar. Pollen, however, is not free yet and the insects carry none. Between 0900 and 1100 the pollen on the 5 tall stamens is released. This coincides with a spreading of these stamens. The pollen bearing surfaces of the tall stamens at this time are presented upwards in a circle that is almost the circumference of the outer edges of the petals. Many pollen-gathering insects forage on the flowers during this time. These include 2 syrphid flies and Xylocopa bees. Others, such as the ctenuchid moth Compstonia and the hesperiids, perhaps are still finding some dilute nectar. The movement of the tall stamens is independent of presence or absence of insect foragers; it was the same in both bagged and exposed inflorescences. However, flowers in the sun opened and presented pollen sooner than flowers in the shade.

About 1130 the male flowers switched from being pollen producers to being both nectar and pollen producers. The tall stamens moved back towards the flower center, thus forming a single column with the 5 short stamens. The short stamens had free pollen by 1200. This coincided with the secretion of some nectar, and visits by a mixed group of foragers (Xylocopa, Palpada, Compstonia, Apis mellifera, and Mischocyttarus). Through the rest of the afternoon a large selection of foragers (mostly nectar gatherers) came to male flowers. These included Compstonia, some hesperiids, 4 species of syrphids, Chauliognathus, Plecia nearctica, Cochliomyia macellaria, and wasps: Mischocyttarus, Anoplius, and Ammophila. The large pollen-collecting bee, Xylocopa, no longer visited, but seemed to be replaced by smaller pollen collectors such as Apis mellifera and Augochloropsis.

Female flowers were also slightly open at dawn. They, too, contain dew and at times a weak nectar. Once, at 0900, 2 flowers that apparently had opened the previous day but had not been visited were found. These contained unusually large volumes of moderately dilute nectar: 0.8 and 1.4 µl of nectar per flower at 29 and 21% sugar concentrations, respectively. While this is unusual, it does explain early morning foraging of hesperiids and dipterans (Cochliomyia macellaria and unidentified species). By 0900 the female flowers are open, but bagged flowers did not secrete nectar until 1200. Visitation during this period is apparently by "accident" or by insects foraging on minute amounts of dilute nectar. However, the stigmas seem to be receptive from early morning.

While the timing of pollen release and nectar secretion in schinus flowers seems quite precisely controlled, the need for it in its newly colonized territory of South Florida is doubtful. A host of insect visitors results in effective movement of pollen from stamen to stigma. Schinus flowering supports many nectar and pollen thieves, but results in good fruit set.

Fruit Set

The results of the 1979 pilot study were that the 2 unbagged branches produced about 100 fruits each, whereas the bagged branches yielded <5 fruits each.

The 1979 results were corroborated by the more detailed study conducted in 1980 (Table 7). About 35% of the unbagged flowers produced fruits, compared to <3% of those that were surrounded by insect exclosures. The 35% fruit set is a relatively high value compared to other species (Stephenson 1981). One tree (#18) produced no fruits, even on unbagged inflorescences.

There are 2 possible explanations of how bagged flowers could have produced any fruits at all. One possibility is that some schinus flowers are perfect, i.e. that they have both female and male parts that are functional, and that self-pollination occurs. Although all schinus flowers observed were unisexual, female flowers have staminodes and male flowers have pistillodes (Fig. 9). It may be that some of these organs undergo complete development, occasionally producing perfect flowers that do not require insect pollination. Such species are called polygamodioecious. This may explain the presence of fruits on a few trees (<1% of the population) that were known to have mostly male flowers, as described in the section on PHENOLOGY.

Another possible explanation is that all open flowers were not removed before bagging, and that some flowers that were bagged had already been pollinated. The early-season flowers yielded fewer fruits (<1% fruit set) than did mid-season or late-season flowers, giving support to this possibility. It is more likely that mid- and late- season inflorescences would have included some already-pollinated flowers than would early-season flowers.

General conclusions are that schinus, although an insect-pollinated exotic, is able to take advantage of several local pollinators. Although its pollination system is not as straightforward as that of some plants, it seems to be effective, resulting in high fruit yield. Although several insect species probably effect schinus pollination, the extremely abundant syrphid fly, Palpada vinetorum, is a likely candidate for the title of chief pollinator of schinus in the study area.

DISPERSAL

Methods

Dispersal of schinus seed was evaluated: 1) by monitoring schinus reinvasion on sites that had been bulldozed, 2) by providing artificial perches for birds, 3) by monitoring schinus seedling appearance in seed traps and soil-seed-storage samples (discussed in a later section), and 4) by observing animals that may disperse schinus.

In spring of 1978 bulldozers were used to destroy approximately 1 ha of schinus-dominated forest along the Hayes Barn Road at the point where the forest bordered unfarmed prairie. Two plots were set up in this bulldozed area to monitor vegetation recovery and possible invasion by schinus. Each plot was 0.5 x 20 m. One plot was oriented east-west, and extended from the border of the unbulldozed schinus-dominated forest into the area that had been bulldozed. The other plot was oriented northeast-southwest, and extended from the border of the unfarmed prairie into the bulldozed area. The vegetation in these two plots was

Table 7. Fruit set in bagged and exposed schinus inflorescences. Flower numbers were estimated by linear regression with panicle length ($r^2 = 0.47$); fruits were counted.

Tree	Bagged No. Flowers	Bagged No. Fruits	Bagged Fruit set (%)	Exposed No. Flowers	Exposed No. Fruits	Exposed Fruit set (%)
Early season (1-28 Oct.)						
1	1,318	3	0.2	3,251	1,211	37.3
2	1,453	14	0.9	1,143	394	34.5
3	2,264	2	0.1	2,536	425	16.8
4	916	8	0.9	2,032	559	27.5
5	1,290	1	0.1	1,195	267	22.3
Peak season (17 Oct.-12 Nov.)						
6	1,322	83	6.3	1,898	668	35.2
7	923	106	11.5	1,025	317	30.9
8	2,085	32	1.5	1,442	650	45.1
9	598	36	6.0	753	228	30.3
10	2,076	128	6.2	417	446	107.0*
11	980	22	2.3	1,031	668	64.8
12	989	25	2.5	959	340	35.5
13	994	46	4.6	1,135	810	71.4
14	2,186	19	0.9	2,912	833	28.6
15	676	7	1.0	1,132	516	45.6
Late season (24 Oct.-13 Jan.)						
16	773	26	3.4	1,236	544	44.0
17	872	68	7.8	1,200	432	36.0
18	1,235	0	0.0	112	0	0.0
19	1,277	41	3.2	2,181	355	16.3
20	1,827	25	1.4	2,422	752	31.1
Total or mean	26,054	692	2.7	30,012	10,415	34.7

* Number of flowers underestimated.

examined periodically until November, 1980. Special care was taken to look for schinus seedlings.

In the spring of 1979 a large area (>100 ha) of schinus-dominated forest extending >2 km south of the Research Center Road was bulldozed. The vegetation was windrowed and burned. Permanent vegetation plots were established by staff of the vegetation ecology group soon after bulldozing was completed. Five plots, each 5 x 20 m, were laid out in a north-south line, with a plot every 500 m. Using the corner posts of these permanent plots as reference points, we laid out 2 schinus colonization subplots within each permanent plot. Each schinus subplot was 0.5 x 5 m, and its long axis was formed by one of the permanent plot borders. One 0.5 x 0.5 m recruitment plot, in which schinus seedlings were counted then removed to evaluate rates of recruitment into the seedling population, was appended to each schinus subplot. These 10 subplots were established in August, 1979 and monitored monthly until June, 1980.

In the area that was bulldozed in 1979 we also set up 5 paired artificial-perch plots, each 1 x 10 m, with 10 m between plots. One plot of each pair was overtopped by a wire, 3.3 m above the ground, strung between 2 poles: the other had a pole at each end, but the poles were not connectd by a wire. Three of the pairs of plots were located between windrowed vegetation, 1 pair was in the area near the road, where care had been taken to avoid bulldozing of Myrica bushes, and the fifth pair was located in a cleared area, not near windrowed vegetation. The orientation of each pair of plots was random, but the members of each pair were parallel. These artificial perches were established in late December, 1979, and the plots were monitored for schinus seedlings, bird droppings, and mammal scat 10 times between then and June, 1980, when the study was terminated.

In 1978 we erected a 9 m extension ladder vertically through the canopy of the old schinus-dominated forest located south of Hayes Barn Road. The ladder was located 100 m south of the road, and was cabled into place, where it remained until late 1980. It served as an observation tower for watching bird movements during the fruiting season. Bird activity in schinus, animal sign, and mammal scat containing schinus seeds or seedlings were noted when encountered throughout the study and on all sites.

Results

No schinus colonized either of the 2 plots established in the area that was bulldozed in 1978. By November, 1980 the vegetation in the plot nearest the schinus forest consisted of a sparse cover (about 80% *Ludwigia microcarpa*) underlain by a well-developed periphyton mat. The plot closest to the unfarmed prairie had a dense cover dominated by *Andropogon glomeratus*, which formed a mat of dead leaves about 0.5 m deep, with live *Andropogon* reaching about 1.5 m. The soil surface was heavily shaded and not covered by periphyton. The dense vegetation on this plot may have hindered seed dispersal, and should lend itself to management by fire.

In 8 of the 10 schinus-colonization subplots set up within permanent vegetation-monitoring plots in the area that was bulldozed in 1979, schinus colonization was very slight. Total seedling counts for each of those 8 plots over the 10-month observation period were: 0, 1, 3, 0, 1, 0, 0, and 0. On the 2 subplots located within the fifth permanent plot, however, schinus recolonization was quite substantial; 23 new (i.e. with cotyledons) seedlings were counted in one subplot and 27 in the other. Total seedling counts (which may include multiple counts of the same individual) on these 2 plots were 46 and 65, but there were never >10 seedlings present on either plot at one time. Some of the seedlings were clustered around the poles marking plot corners, and may have been dispersed to those points by birds that used the poles as perches. Schinus dispersal is readily accomplished into newly bulldozed sites if all nearby seed sources are not eliminated, but this dispersal is patchy, not uniform. In some areas seedlings recolonize at a density of at least 4 per m^2: more than enough to produce a schinus-dominated stand.

Schinus also recolonized the plots located beneath artificial perches, but no faster than it recolonized paired plots not overtopped by perch wires. Counts of new seedlings (i.e. with cotyledons) for the 6-month study period, summed over all 5 pairs of plots, were 49 seedlings on plots not overtopped with a wire and 32 seedlings on plots with a wire. The data were quite variable, and differences between plot types were not statistically significant. Although the perches did not attract birds that effectively dispersed schinus (even though birds were observed using the perches), these plots reconfirmed the observations derived from the subplots within the permanent plots: schinus recolonization is effective after bulldozing, but quite variable from point-to-point.

Catbirds (Dumatella carolinensis) are commonly observed feeding on schinus fruits. They are present each year, and may be important dispersal agents, but they spend most of their time in woodlands, and seldom venture into open fields. We know that raccoons (Procyon lotor) consume schinus fruits, and assume that opossums (Didelphis virginianus) do also. Mammal stools are sometimes encountered that contain hundreds of germinating schinus seeds (Fig. 13). Mammals may not only disperse schinus seed, but also effectively "plant" it with nutrient-rich fecal material, thus perhaps giving the seedlings a competitive advantage over other species. Germination of seeds in mammal stools may account for the multiple-stemmed habit of some schinus (although it can be caused by frost-kill of the main trunk as well), and for our early observations that some schinus trees had main branches with female flowers and main branches with male flowers. Entire schinus inflorescences frequently dehisce, depositing dozens of seeds in a small area. These piles of seeds also form multiple stemmed clumps of schinus, but are not dispersed far from parent trees, as are seeds contained in scat. Vast quantities of schinus seed fall to the ground beneath female trees, but this seed is not dispersed far. Some of it is moved by water, but water levels are usually low at the time of schinus seed-ripening. Animal dispersal of schinus is certainly more important than dispersal by water or gravity.

Fig. 13. Germination of >200 schinus seedlings from a mammal stool.

Probably the most spectacular dispersal of schinus seed is effected by robins (Turdus migratorius). In early 1977 (a cold winter), before our studies began, robin flocks were very evident in the schinus forests within Everglades National Park. In the winters of 1978 and 1979, however, there were no massive buildups of robin flocks in those same schinus-dominated forests. In the winter months of early 1980, however, the robin flocks returned again, and we had ample opportunity to observe their behavior. The robins eat vast quantities of schinus fruit, and tend to exhaust the food supply in one area before relocating. They also move among several kinds of ecosystems, including both schinus-dominated successional forests and pinelands. There can be no doubt that they disperse large quantities of schinus seed into non-schinus-dominated ecosystems, especially those that contain perches. Such communities include pinelands, hammocks, and roadsides beneath electric wires.

Unlike dispersal by catbirds, raccoons, and opossums, dispersal of schinus by robins is not predictable year after year. When they are present, their activities are spectacular, and they undoubtedly move large amounts of schinus seed into habitats it would never reach otherwise. Their presence--like that of droughts, frost, and hurricanes--is not an annual phenomenon. When they are present, however, they may move more schinus seed than all other dispersal agents combined.

GERMINATION

Methods

Germination studies were set up in a greenhouse at the University of Florida, Gainesville in early May, 1978. We tested 3 species: schinus, *Myrica cerifera* (wax myrtle), and *Ilex cassine* (dahoon holly). The schinus seeds were harvested by us in the Hole-in-the-Donut in April, which is near the end of the period of schinus fruit availability. We harvested fruits from 2 trees and studied them separately to enable us to evaluate tree-to-tree variability. The *Myrica* and *Ilex* seeds were provided by the Resource Management staff in the Everglades National Park.

A portion of each of the 4 batches of seed was subjected to 1 of 5 treatments: 1) control, no treatment, 2) mechanical scarification by shaking them with rocks in an incubator at 25° C for 3.5 hours 2 days prior to the beginning of the germination test, 3) chemical scarification (95% H_2SO_4) for 15 min, 4) same for 30 min, and 5) same for 60 min. For the first 2 treatments 400 seeds from each batch were used, while 100 seeds from each batch were subjected to each of the 3 acid scarification treatments. The seeds were divided into lots of 25 and each lot was placed on moist filter paper in a Petri plate. The plates were then assigned to randomly selected locations on a greenhouse bench. We treated all plates once with a dilute captan fungicide solution following an early fungal outbreak; no further treatment was necessary. Germination was monitored every 3 days for 130 days.

Results

Schinus germination was tested for seeds from 2 different trees, and there were significant differences between them (Fig. 14). Germination was about twice as great for seed from 1 of the trees (about 60%) as it was for the other (about 30%).

Germination of schinus was quite rapid, and was concentrated primarily in the first 20 days of our 130-day-long study. No germination occurred after about 55 days. Germination of the less vigorous of the 2 lots of schinus seed was not enhanced by mechanical or chemical scarification. Seed from the other tree, however, responded postively to 15 and 30 min acid treatments (95% H_2SO_4), but not to 60 min of acid soaking nor to mechanical scarification.

The schinus seeds were gathered after nearly all trees had already dropped their seed. Therefore, the estimates of germination capacity may be lower than the true potential for the species. Even if the values are low, they indicate that schinus has a tremendous reproductive potential. The seed crop on a mature female is enormous, and a germination of 30 to 60% in the field would result in a vast number of seedlings.

In addition to schinus seeds, seeds of wax myrtle and dahoon holly, both of which are desirable native species that might be managed to enhance their competitive ability with schinus, were also germinated. Both

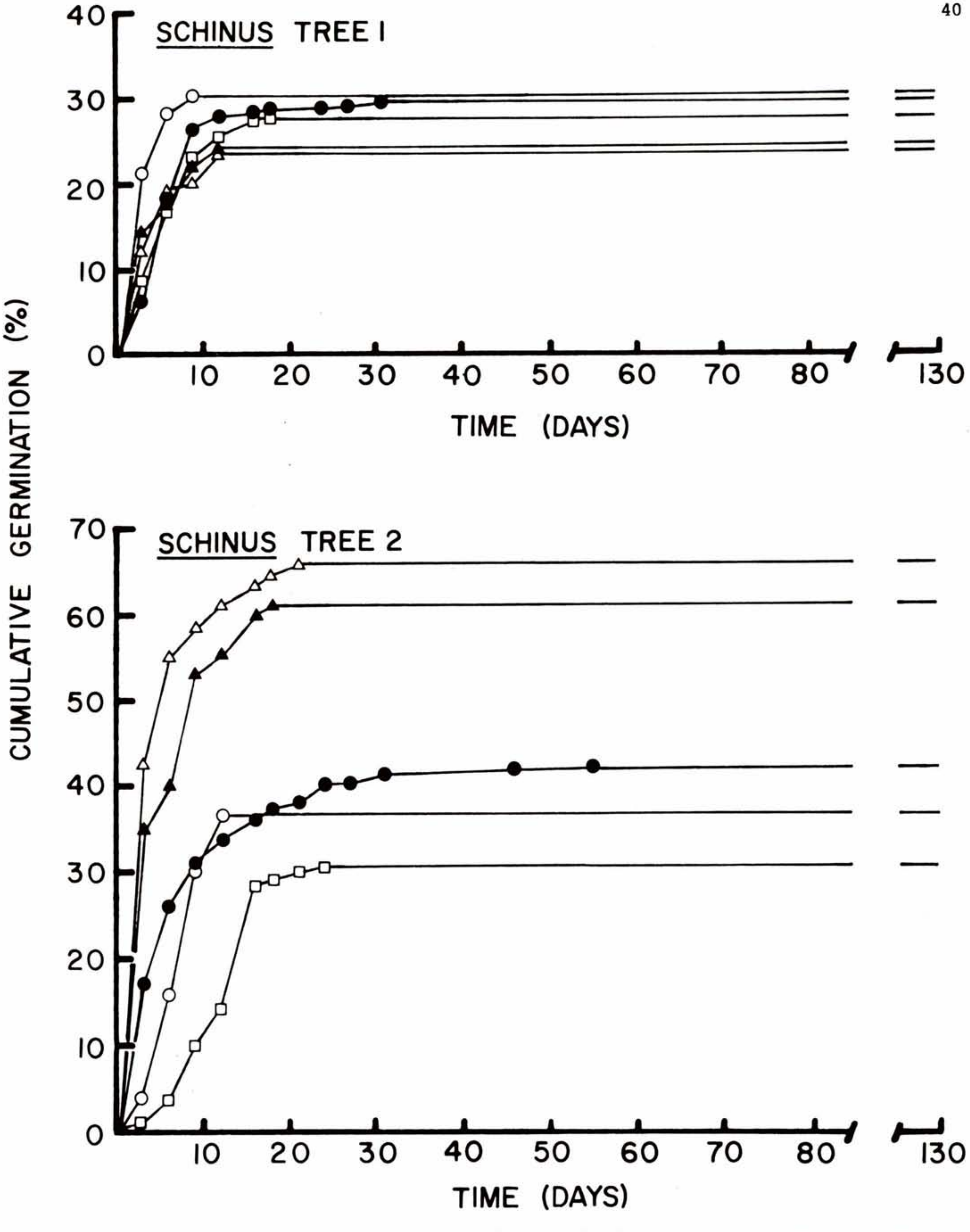


Fig. 14. Time course of schinus germination in the laboratory. Treatments were: controls (solid circles); mechanical scarification (open squares); and chemical scarification with acid for 15 min (open triangles), 30 min (solid triangles), and 60 min (open circles).

species germinated more slowly than schinus (Fig. 15). Wax myrtle did not germinate much before 10 days and germination was still observed 80 days after the start of the experiment. Holly was even slower; almost no germination occurred in the first 3 weeks. Also, germination was lower for these species than it was for schinus. Wax myrtle did only about as well as the poorer of the 2 schinus seed lots, even under the best treatments. Holly never even reached 15% germination.

These species responded to some of the scarification treatments. Holly germination was tripled by the intermediate-length acid treatment (30 min) and increased less markedly by the 15-min and 60-min treatments. Mechanical scarification did not increase holly germination; in fact, it may have decreased it slightly.

Wax myrtle seed did not respond to the 15-min acid treatment, but it did respond positively to all other scarifications. The longer the acid bath, the greater the wax myrtle germination. Mechanical scarification was even more effective. It increased not only the amount of germination but also the speed.

Both of these species would be characterized as having poor germination, at least when compared with schinus. The seed lots we treated had been harvested well before our study, so our results may reflect a short shelf life. If either of these species is to be grown in vast quantities by direct seeding, however, the results indicate that a tremendous quantity of seed would be required to insure successful seedling establishment.

SEEDLING DYNAMICS

Methods

Schinus seedling dynamics, including germination, mortality, and population density, were monitored approximately biweekly for >2 yr in 4 schinus-dominated forests. At each site we established numerous (10 to >20) permanent plots where we counted schinus seedlings, distinguishing those with and without cotyledons.

Ten of the plots at each site were arranged in 5 pairs, and each pair was located at 40 m intervals along a 200 m transect at each site, beginning at least 10 (usually 20) m inside the site boundary. These plots were paired because of the rows and furrows that remained from earlier farming practices. The rows and furrows were oriented east-west, perpendicular to the direction of flow of surface water. One member of each pair was placed along a row top, and the other was placed within 1-2 m of the first, along the bottom of a furrow. These plots were 0.5 m wide by 4 m long. To estimate recruitment of new individuals into the population sampled by each pair of plots, a 0.5 m by 5 m recruitment plot was established perpendicular to the long axis of each pair of row-furrow plots. New schinus seedlings (i.e., with cotyledons) found in these recruitment plots were counted, then removed. This enabled us to monitor germination and recruitment into the population.

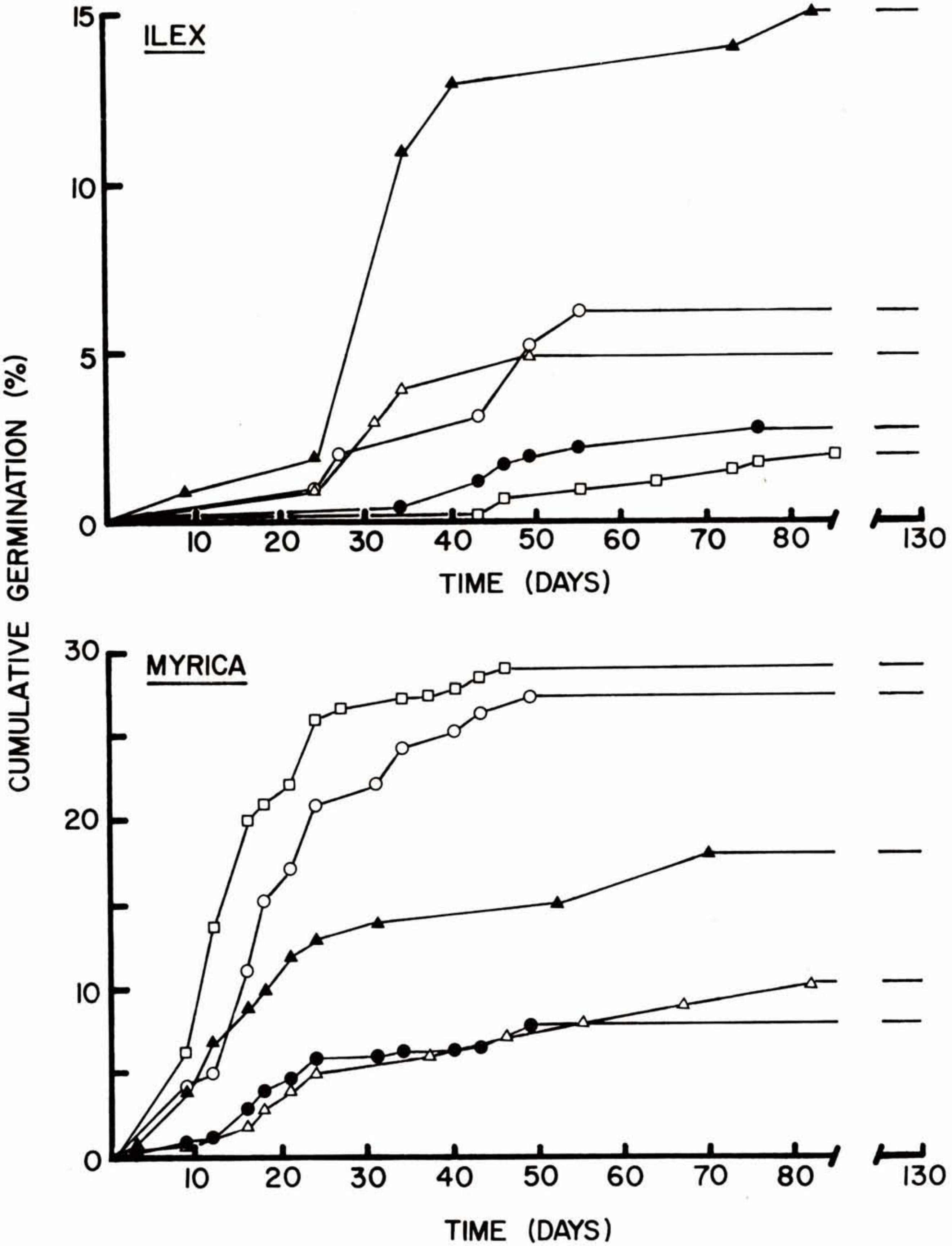


Fig. 15. Time course of germination of Ilex cassine and Myrica cerifera in the laboratory. Treatments were: controls (solid circles); mechanical scarification (open squares); and chemical scarification with acid for 15 min (open triangles), 30 min (solid triangles), and 60 min (open circles).

We wished to begin the study with an initial schinus seedling population size >1000. In the Myrica-schinus woodland the 10 row-furrow plots did not include >1000 schinus seedlings, so 7 supplemental plots were established in areas of high schinus-seedling density. Each supplemental plot was 0.5 m by 5 m, and a 0.5 m by 0.5 m recruitment plot was appended to the side of each, midway along its long axis.

Two more supplemental plots had been established in December, 1975, just inside old schinus forest no. 1. One plot, located 4 m from the road, was 2 m by 1 m; the other, located 15 m from the road, was 2 m by 2 m. These plots were set up before our study began in order to monitor schinus seedling densities and to determine whether or not schinus could successfully reproduce in its own shade. The seedlings on these 2 plots were counted sporadically until spring, 1978, after which they were counted each time the other seedling plots at that site were monitored.

Results

Germination was determined directly by counting new (i.e., with cotyledons) schinus seedlings in recruitment plots located near or contiguous to the inventory plots in each of 4 schinus-dominated forests. Mortality rates were calculated by algebraically subtracting germination rates from rates of change in seedling density in the inventory plots. Germination rates of schinus seed and mortality rates of young schinus seedlings are shown for each of the 4 schinus-dominated study sites in Fig. 16. Each value is a mean of all plots inventoried on each site (n = 10 to 17 plots, covering 32.5 to 39.3 m^2), including both the impartially distributed plots located on old rows and furrows (10 such plots per site) plus plots deliberately located in areas of high schinus seedling density to assure an initial sample size of >1,000 schinus seedlings (0 to 7 such plots per site).

Germination on all sites was concentrated from November to April each year, with most germination occurring in January and February. Germination rates $>100/m^2 \cdot 15$ days were commonly encountered, and the ground beneath mature female schinus trees was often carpeted with seedlings.

Although seed dispersal of schinus is remarkably synchronous, we did observe some schinus germination as late as May and June. This may have been late germination of the previous crop of seeds, or it may have been germination of seeds produced during the secondary (and very minor) season of fruit production, as described in the section on PHENOLOGY. Similarly, substantial germination of schinus was once encountered in 1 of the old schinus forests (no. 2) in late October and early November, but we were unable to determine whether it resulted from early maturation of fruits on a precocious female (none were observed in the immediate area), or delayed germination of seeds that had lain on the ground since the previous seed drop many months earlier.

Unlike germination, mortality is not concentrated in a particular season, but occurs throughout the year. Schinus seedling mortality probably results from a mixture of density-dependent factors (e.g., intraspecific competition, some kinds of herbivory) and density-independent factors (e.g., environmental factors, limb fall, mammal trampling), so

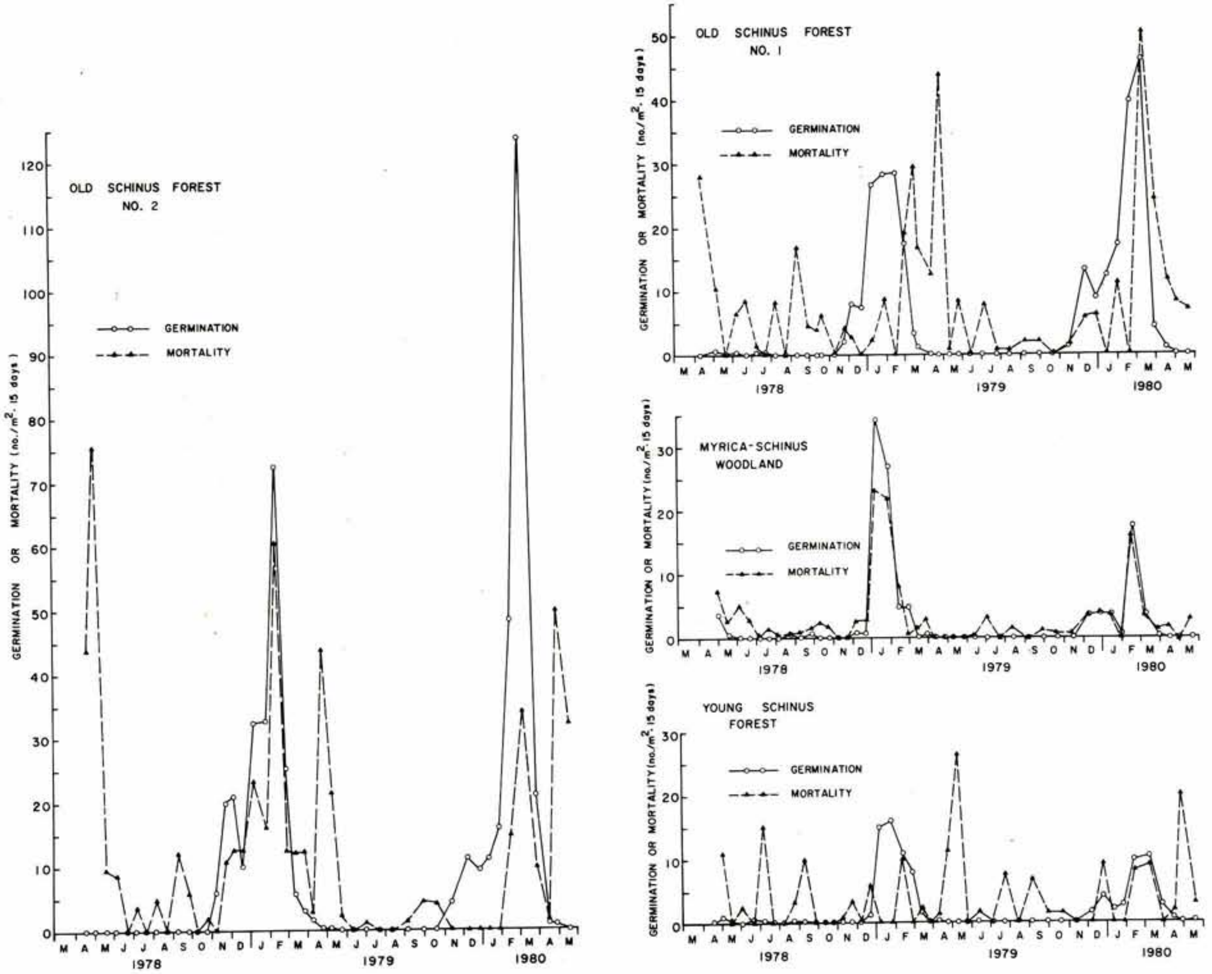


Fig. 16. Germination and mortality of naturally occurring schinus in 4 schinus-dominated forests.

an annual pattern is difficult to unravel. On many sites there is a close correspondence between germination and mortality rates: the greater the germination the higher the mortality, and mortality closely tracks (slightly lags, usually) germination (Fig. 16).

The environmental factor that seems to be responsible for most schinus-seedling mortality is water: either too much or too little. The driest time in the study area is late May, just prior to the start of the summer rains. This driest period comes soon after the large annual pulse of schinus germination, and results in the death of many schinus seedlings, especially on drier sites, such as those occupying former pinelands. July, August, and September, on the other hand, are extremely wet months, and most of the study sites have considerable areas covered by standing water at that time. Although schinus seedlings can tolerate substantial amounts of water (and even complete submergence), the summer floodwaters probably account for much schinus seedling mortality.

On April 24, 1979, South Florida received an unusually large and early storm; it deposited 23.21 cm of rain on the research area. Water levels rose from their lowest points of the year to their highest levels of the year within hours, and this had 2 impacts on the mortality of young schinus seedlings. First, on the driest sites (e.g., former pinelands) this early deluge probably reduced mortality by saturating the soil before the peak of the dry season. Second, on the wettest sites (e.g., former prairies and sawgrass glades) many schinus seedlings undoubtedly drowned. This mortality peak caused by the sudden spring flood is conspicuous on the mortality graphs for the 3 sites on former prairies (old schinus forests nos. 1 and 2 plus young schinus forest), and conspicuously absent from the graph for the Myrica-schinus woodland, occupying drier former pinelands (Fig. 16). Similar, though less dramatic, mortality followed a storm in spring of 1980.

When the study was initiated, we suspected that microsite differences caused by farming practices (specifically, the topographic differences caused by the construction of elevated rows separated by furrows) might result in differential schinus establishment rates on high and low microsites. There may be seasonal differences in germination and mortality rates may differ between them, but the density of schinus seedlings did not differ significantly between topographic highs or lows in either the old schinus forest or the young schinus forest, the 2 sites where we were able to test for microsite differences (Fig. 17). Some of the peaks of seedling densities in the furrows, corresponding to the post-dispersal germination peak, resulted from schinus-seeds rolling off the rows and accumulating in the furrows.

The net result of dispersal, germination, and mortality is the density of seedlings on the forest floor, and this is shown for the 4 study sites in Fig. 18. During the 2 yr that seedling densities were monitored, mean densities in the 4 schinus-dominated forests ranged from <10 to >200/m^2. The most marked seasonal trends in schinus seedling abundance were evident in the 2 old schinus forests, where densities peaked in February-April then plummeted to relatively constant, low densities until dispersal and germination of the next crop of seeds at the end of the year.

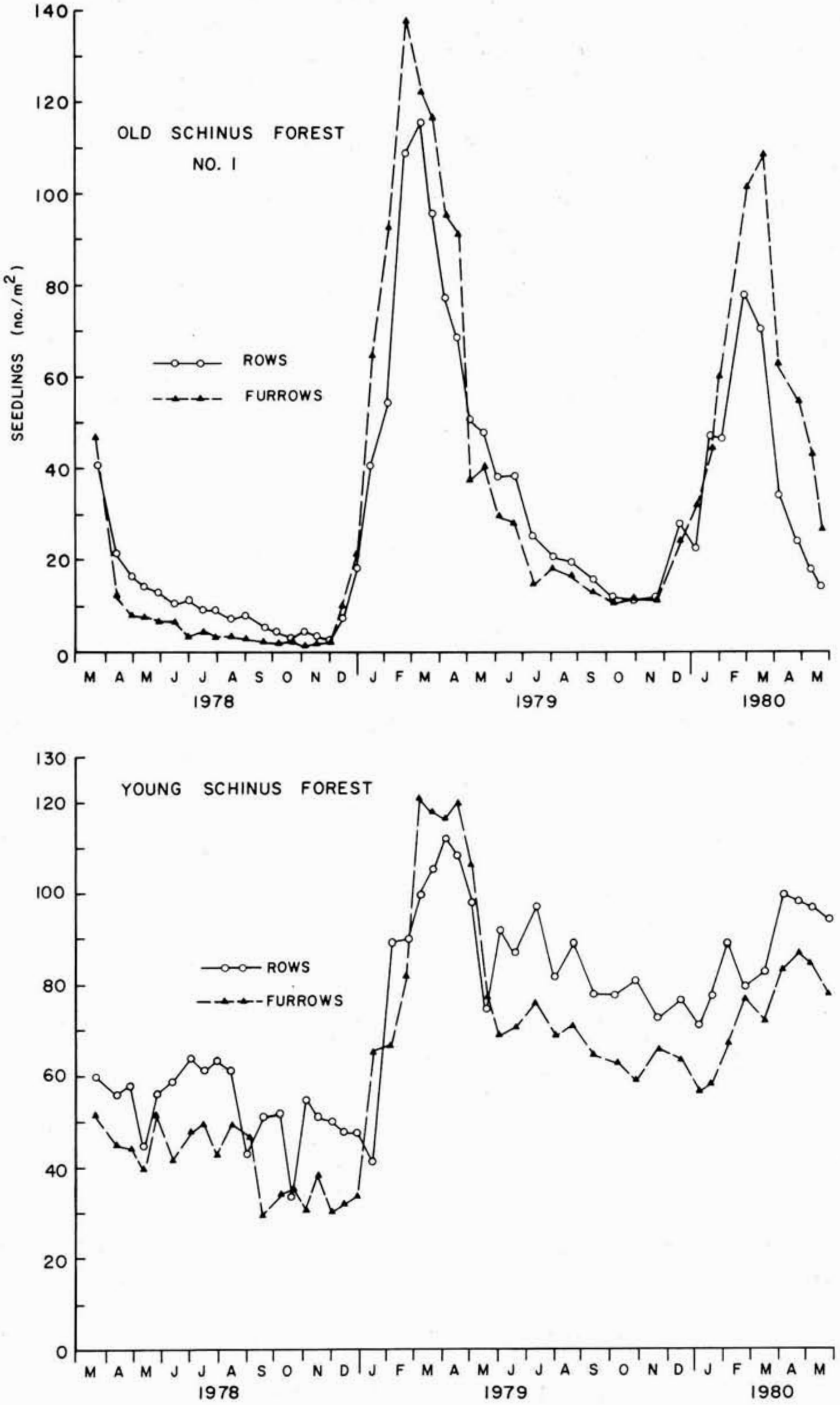


Fig. 17. Time course of schinus seedling density on rows and furrows in schinus-dominated forests occupying former farmland.

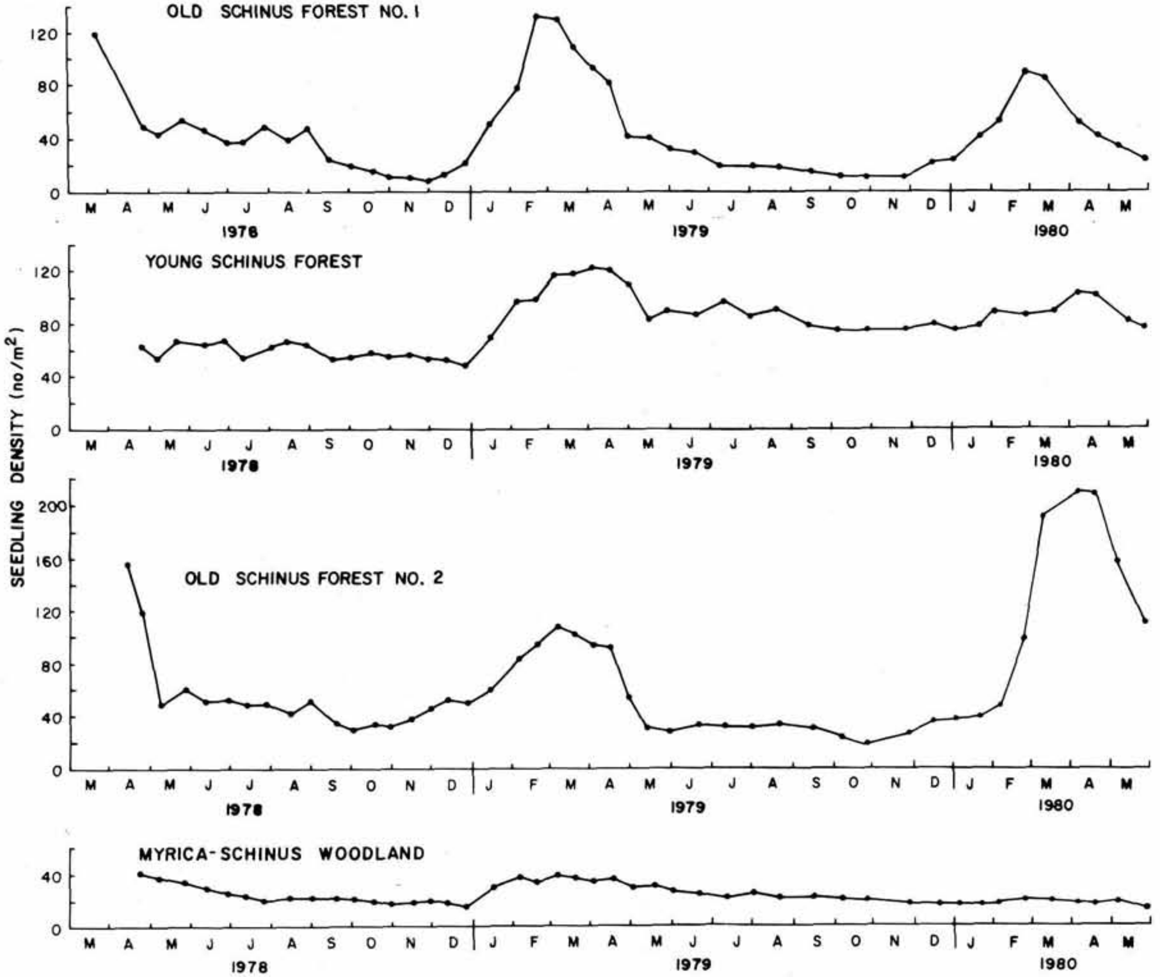


Fig. 18. Time course of schinus seedling density in 4 schinus-dominated forests.

Seasonal ups and downs of schinus seedling densities on the other 2 sites (Myrica-schinus woodland and young schinus forest) were less dramatic than those of the older schinus forests (Fig. 18). In the young schinus forest there was a high density of seedlings present throughout the year. Furthermore, mean seedling density increased from about $60/m^2$ in 1978 to about $80/m^2$ in 1979, indicating that this site may still be susceptible to new colonization. The overstory in this stand is quite open, and abundant light reaches the forest floor, thus permitting large numbers of new seedlings to survive.

In the Myrica-schinus woodland (the driest schinus-dominated study site), seedling densities were low and relatively constant throughout the year. Except for modest increases following seed dispersal and germination, there are no evident trends in seedling abundance during the year on this site. The overstory is dense, Myrica tree falls are common, the Myrica leaf litter is deep and dries readily, and Myrica is allelopathic to schinus (Dunevitz and Ewel, 1980). These factors apparently interact to result in relatively constant, low densities of schinus seedlings.

The density of seedlings on the long-term supplemental plots in old schinus forest no. 1 (Fig. 19) verify the fact that schinus does germinate under dense schinus shade and that germination does not decrease with time.

Although seedling densities drop to low levels during the summer months, it is important to note that there are always some seedlings present on all 4 sites. Thus, canopy disruption at any time (even during the summer hurricane season, for example) could open the way to schinus site recapture should sufficient moisture exist.

SEEDLING GROWTH AND SURVIVORSHIP

Methods

The growth and survival of naturally occurring schinus seedlings were monitored for >2 yr at 5 sites. These sites included the 4 schinus-dominated forests where schinus seedling dynamics were measured, (see previous section), plus an area on the north side of the Research Center Road, northwest of the northern-most missile base, where schinus control had been attempted.

In the 4 schinus-dominated forests, all schinus seedlings >10 cm tall that were inside the plots established to monitor seedling dynamics were tagged using aluminum labels attached with loose-fitting wires. In the schinus-control area, seedlings were tagged on 2 plots, each 0.5 by 4 m. The number of seedlings initially tagged at each site ranged from 9 to 176. On November 2, 1978 the number of tagged seedlings was standardized to 70 per site. On 2 sites additional seedlings were tagged to increase the sample size to 70. These seedlings were located near the permanent plots where other tagged seedlings were located. On the other 3 sites the number of tagged seedlings was reduced by randomly selecting 70 of the tagged seedlings.

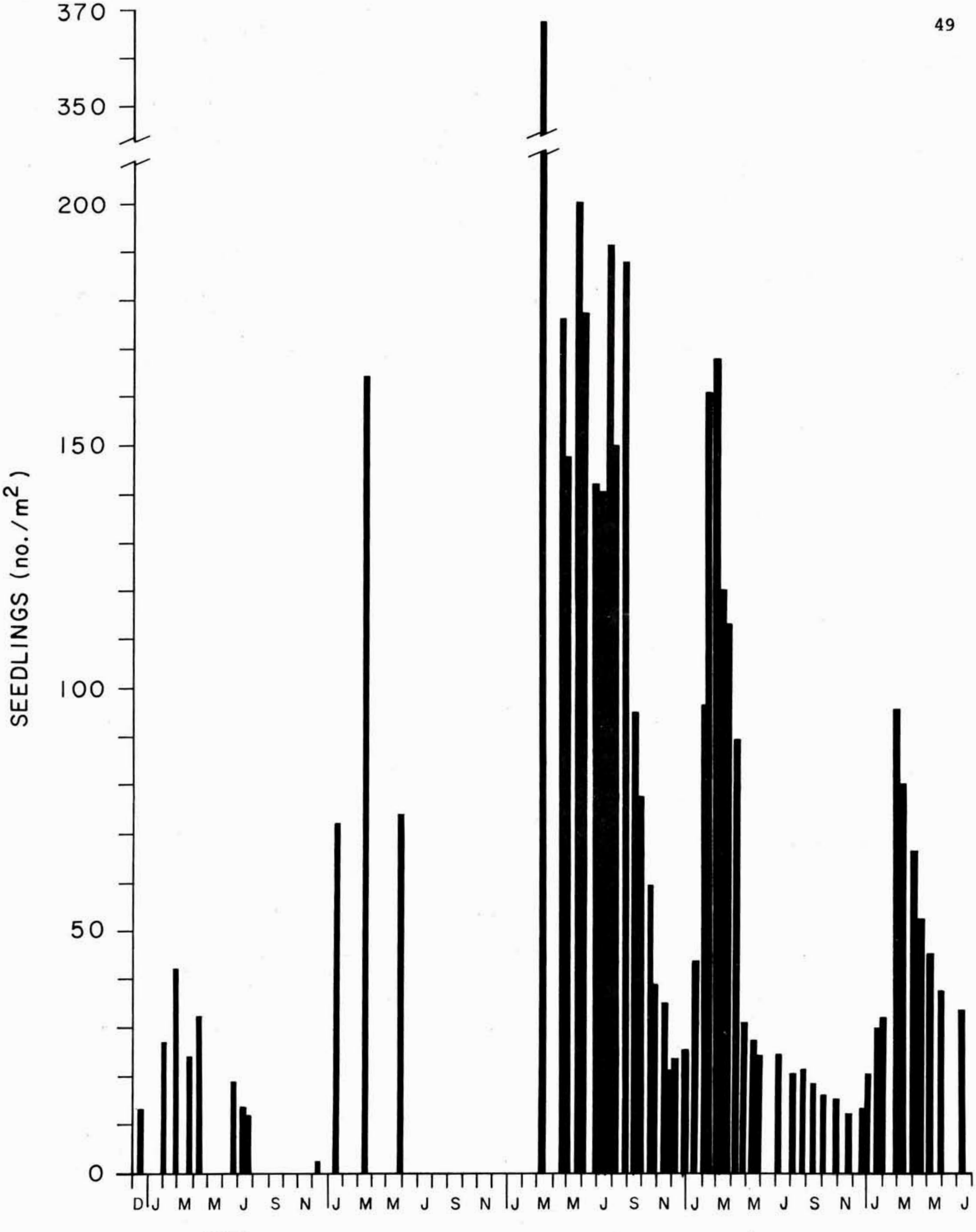


Fig. 19. Schinus seedling density in 2 long-term study plots, old schinus forest no. 1. Blanks indicate no observation, not absence of seedlings.

The height of each seedling was recorded approximately monthly to the nearest cm. Dieback of seedling tops and stem breakage were included in growth calculations as negative growth. Trees that died in the interval since the previous measurement were excluded from the growth calculations. Trees thought to be dead, but which resprouted were re-included in the growth measurements beginning with the first growth-measurement interval following the first time they were observed to resprout.

To determine the response of naturally established schinus seedlings to canopy disruption, plots were established in each of 4 schinus-dominated forests. In each forest 2 mature, female schinus trees were chosen. Because this study was also established to monitor gap capture by new schinus seedlings, care was taken to select mature females that were surrounded by male schinus trees or by other tree species, and not by other female schinus trees.

Four plots were established radiating outward from the base of each schinus trunk. Plot orientations were NE, SE, SW, and NW, so they crossed the east-west rows and furrows at 45°. Each plot was 0.5 m wide and either 5 or 6 m long, depending on the crown width of the overstory schinus tree. A 0.5 by 0.5 m seedling recruitment plot was appended midway along the side of each plot. In the plots beneath each of these 8 female schinus trees, 20 seedlings >10 cm tall were tagged. Their height and survival were monitored monthly through October, 1980.

On November 7, 1978, 1 of the 2 mature female trees on each site was randomly selected and killed by girdling its trunk, followed by herbicide (2,4-D) application to the frill.

Results

The survivorship of naturally established schinus seedlings was very high at all 4 schinus-dominated sites (Fig. 20). Mortality was greatest in 1 of the old schinus-dominated forests (no. 1), but even there nearly 1/3 of the tagged seedlings survived over the 22-mo monitoring period. In the 2 other dense forests (the Myrica-schinus woodland and schinus forest no. 2), nearly 2/3 of the established seedlings survived, and there was almost no mortality in the two vegetations that were youngest: the young schinus woodland and the schinus control area.

Such high survivorship of seedlings is an unusual characteristic, even for mature-forest tree species. It is extremely rare to encounter such high survivorship in weedy species (such as schinus in South Florida). The tenacity of its seedlings makes schinus an especially difficult species to deal with, as its seedlings seem to be able to survive for a very long time in the dense shade of an older stand.

The height growth of naturally established schinus seedlings on 5 sites is summarized in Fig. 21. The confidence limits shown around each height measurement are 1 standard deviation of the growth that occurred in the interval preceding the height remeasurement. The mean height of the 70 seedlings tagged at each site on November 2, 1978 was taken as a baseline mean seedling height. The cumulative mean growth (± 1 standard deviation) of surviving seedlings was added to that mean height for each

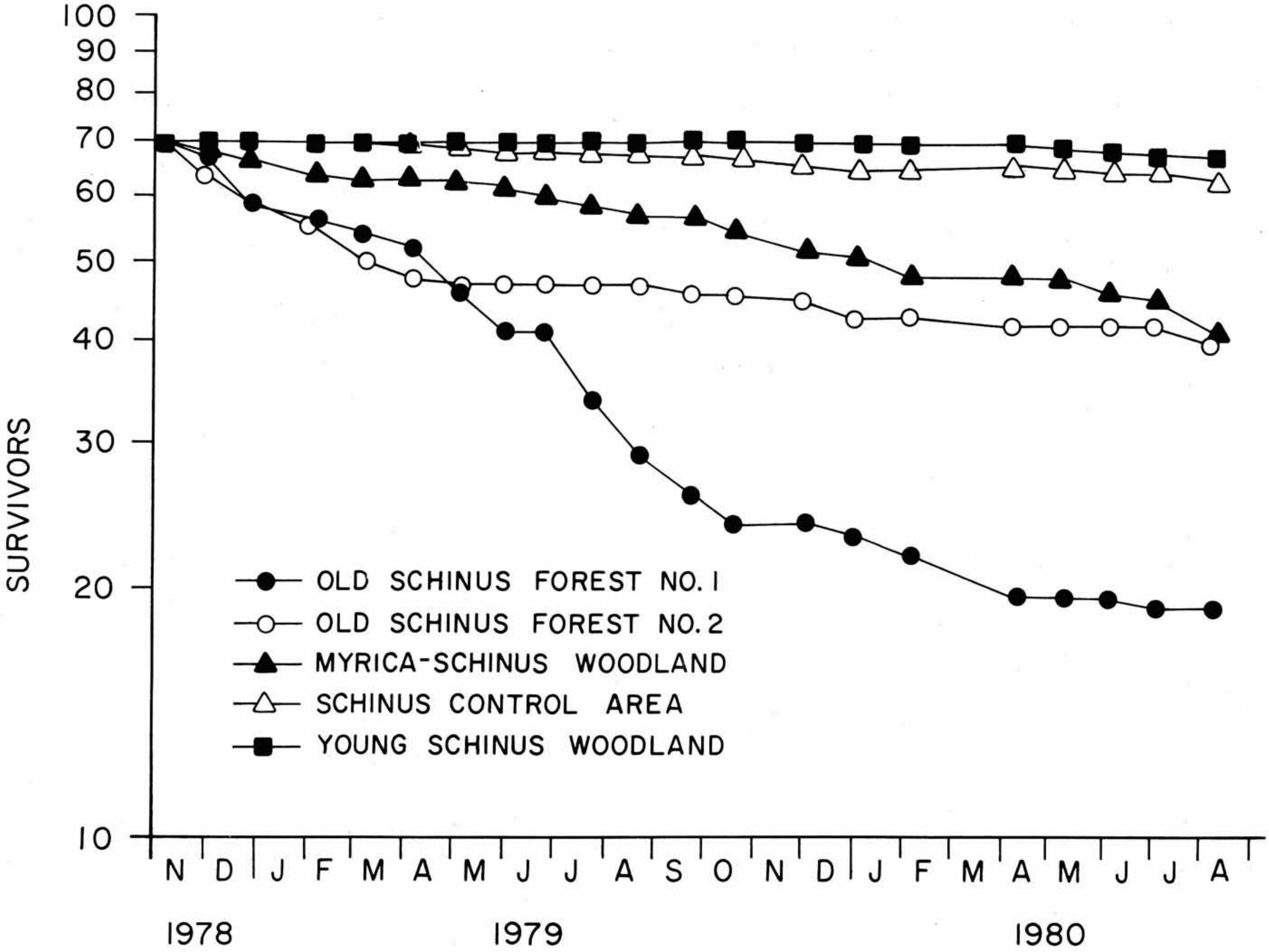


Fig. 20. Survivorship of naturally occurring schinus seedlings in 4 schinus-dominated forests. In Nov., 1978 all seedlings were >10 cm tall.

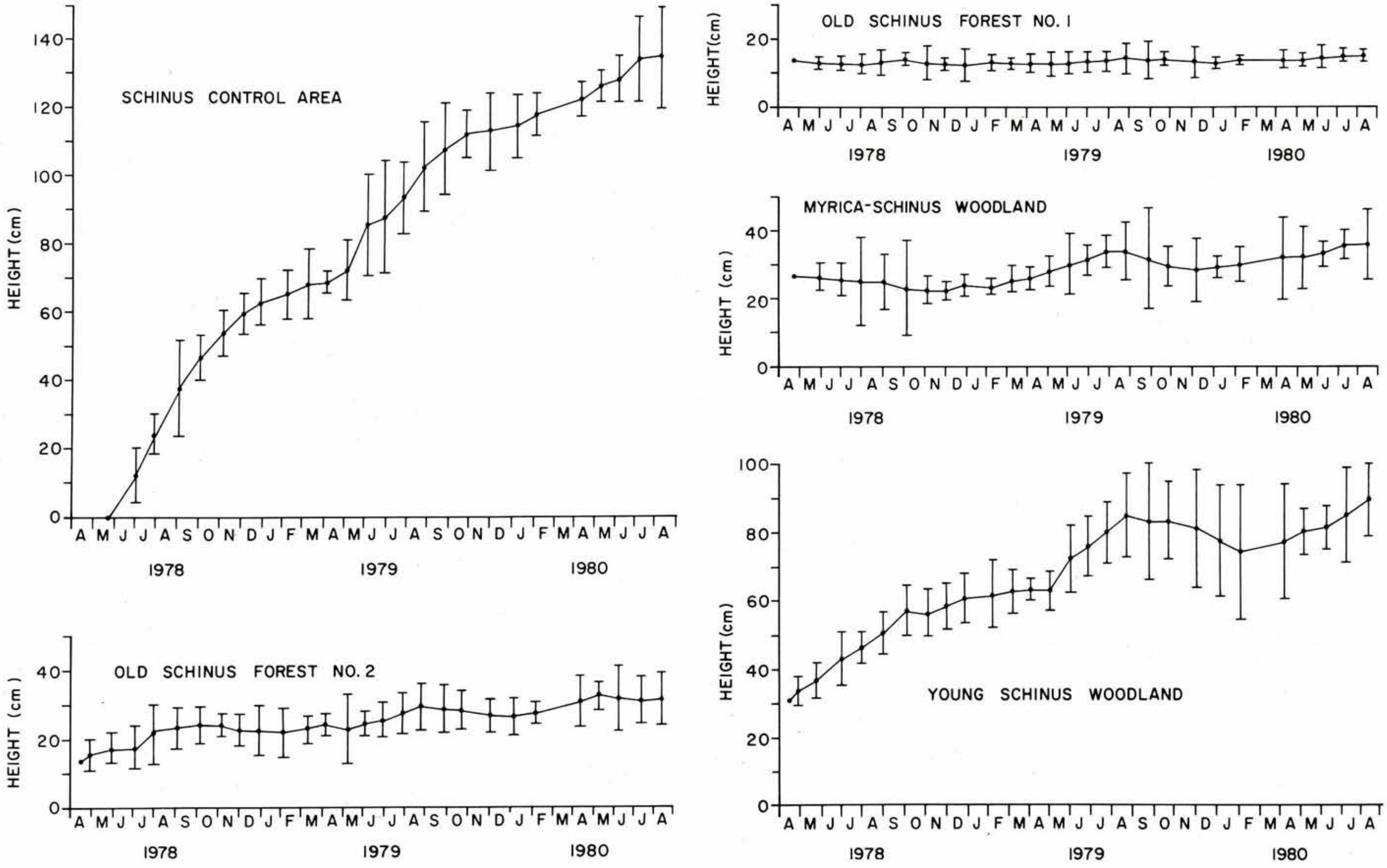


Fig. 21. Height growth of naturally occurring schinus seedlings at 5 study sites. Vertical bars are 1 standard deviation of growth for preceding interval.

measurement interval after November, 1978 and subtracted from that height for each interval prior to November, 1978.

In the 3, older schinus-dominated forests (old schinus forests nos. 1 & 2 plus the Myrica-schinus woodland), understory schinus seedlings grew extremely slowly: from almost nothing to only a few cm per year. At the 2 sites where the vegetation was more open, however, the response was very different. In the young schinus woodland, schinus seedlings grew about 0.3 m per year, and in the area where schinus control was attempted schinus seedlings grew an average of 0.5 m per year.

On 3 of the 4 sites where artificial gaps were created, the understory schinus seedlings responded to gap creation with vigorous height growth (Fig. 22). In schinus forest no. 1 the trees in the gap did not respond to the opening because the gap quickly closed due to ingrowth of limbs from surrounding male schinus trees. On that site growth of schinus seedlings in the gap did not differ from that of seedlings under the control tree. On the other 3 sites, schinus seedlings in gaps were more than twice as tall as seedlings under control trees after 2 yr.

Schinus seedlings are inordinately tenacious and exhibit tremendous growth plasticity. They survive in dense shade, where their growth rates approach zero for >2 yr. In open vegetation they are extremely competitive and vigorous, and under such conditions their growth rates are very rapid. Even suppressed understory schinus seedlings respond quickly to canopy disturbance, and are capable of capturing gaps created by the death of overstory parent trees.

INVASIBILITY

Methods

Seed Introduction

To test the ability of schinus to invade various ecosystems, 2 seed-introduction experiments were run: one in 1979 and the other in 1980. In 1979, schinus seeds were introduced into 17 ecosystems in January, February, March, April, and May. The ecosystems included 3 mature communities (glade, pineland, and hammock); 3 woodlands containing abundant, reproductively mature schinus trees; and 11 areas occupied by successional vegetation <7 years old, including 9 sites that were disked in 1975. At each introduction, 3 points were randomly selected along a transect (usually 200 m long), and 800 schinus seeds were placed in a 0.5 by 0.5 m plot at each point. At monthly intervals thereafter, through August, 1979, the number of germinated schinus seeds at each point was counted. Once counted, seedlings were uprooted and discarded. To correct for the natural dispersal of schinus seeds onto these seed-introduction plots, auxillary plots, each 0.25 by 0.5 m, were appended to each side of each seed-introduction plot. The seedlings that appeared in these auxillary plots were assumed to result from naturally dispersed schinus seed, so the number of seedlings in the auxillary plots was multiplied by 0.5 (to correct for the difference in area between the seed-introduction plot and the auxillary plots), then subtracted from the number of seedlings in the seed-introduction plot.

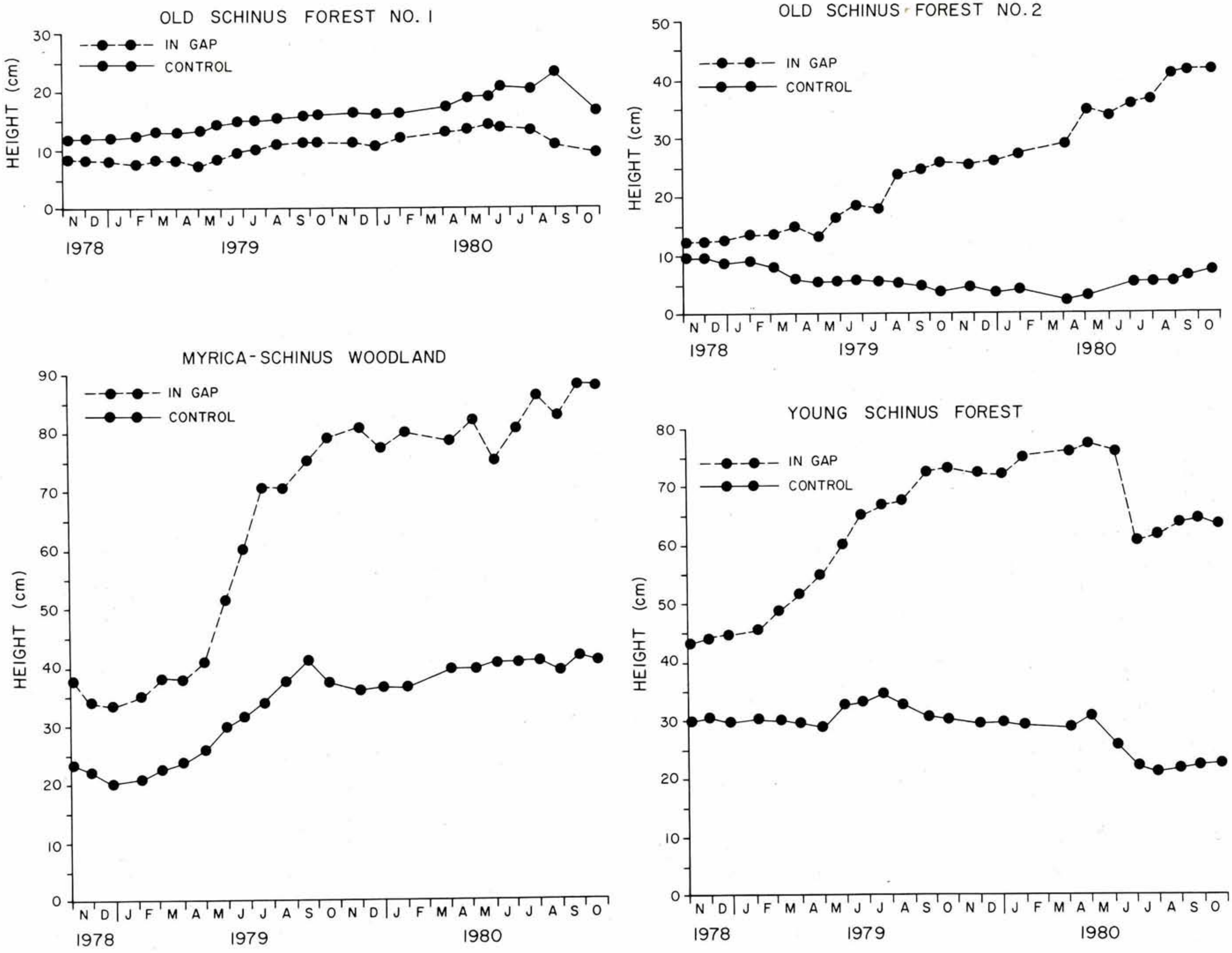


Fig. 22. Height growth of naturally occurring schinus seedlings in gaps and beneath forest canopies.

In 1980, schinus seeds were introduced into 9 ecosystems in January, February, and April. Sample points were chosen as in 1979, but 1000 schinus seeds were placed in each of the 3 sample plots per site. Also, the auxillary plots were separated from each seed-introduction plot by a 0.25 m buffer strip to assure that introduced seeds that rolled out of the seed-introduction plot were not tallied as naturally occurring. The germinated seeds were counted monthly, until October, 1980, and counts were corrected for germination of naturally dispersed seed, as in 1979. In 1980, however, counted seedlings were not uprooted. Thus, the 1979 experiment emphasized the timing of germination of introduced seed, whereas the 1980 experiment emphasized the survival of seedlings that resulted from introduced schinus seed.

Seedling Transplants

To further test the ability of schinus to invade various ecosystems, the crucial initial stages of seed germination and seedling establishment were bypassed, and well-developed schinus seedlings were transplanted into 10 sites. The 10 sites included 3 mature ecosystems, (glade, pineland, and hammock), 4 schinus-dominated forests, and 3 successional stands <6 years old. Schinus seedlings for transplant were grown from seed in plastic conical containers about 20 cm deep and 4 cm in diameter, in marl soil taken from the young (1975) succession site. Most seedlings were 10 to 30 cm tall when outplanted. Seedlings were outplanted in September, October, and November, 1978, and June and August, 1979. On each planting date, 10 seedlings (8 in June, 1979) were transplanted onto each of the 10 sites. They were planted, 2 per location, at 5 randomly selected intervals along a 200 m transect. Their growth and mortality were monitored monthly through August, 1980.

Results

Seed Introduction

The results of the 1979 seed-introduction experiment are summarized in 2 tables: Table 8, containing data from 9 communities on land cleared in 1975, and Table 9, containing data from 8 other communities, including 3 mature ecosystems, 3 schinus-dominated woodlands, and 2 successional stands. Germination in the field ranged from <1% to >30%. This compares with the range of 20 to 30% schinus germination normally attained in laboratory and greenhouse conditions. On most sites germination was greatest within 30 days following seed introduction, and declined thereafter. A tiny proportion of the seed (<0.05%) retained its viability for 5 months, but no seed germinated after having been on the ground for 6 months. Some germination occurred on each of the 17 sites, but there was considerable variation among sites and among sample points within sites.

Germination was greatest in February and March, and lowest in April, July, and August. There was a delayed burst of germination on 2 of the 1975-succession plots (nos. 1 & 2) in late April to early May, following the unprecedented rainfall (>23 cm) of April 24-25. These 2 1975 succession plots are in the drier, northern end of the study area, on former pineland. The dry season rainfall deluge apparently stimulated

Table 8. Germination of schinus seeds introduced in 1979 to 9 plots in successional vegetation on land that was cleared in 1975. On each of the 5 seed-introduction dates, 2,400 seeds were placed in each plot, 800 at each of 3 locations. Numbers are seeds that germinated in the interval since the last count.

Jan 11-12	Feb 13-14	Mar 9	Apr 19-20	May 18	Jul 12	Aug 15	Plot
SEEDED	36	8	1	7	1	0	1
	561	28	10	11	1	0	2
	42	16	4	0	0	0	3
	55	4	2	0	1	0	4
	5	1	2	0	0	0	5
	92	6	3	0	1	0	6
	62	24	3	0	0	0	7
	0	3	0	0	0	0	8
	11	2	3	0	0	0	9
	SEEDED	9	3	61	3	0	1
		9	3	17	2	0	2
		129	3	0	0	0	3
		9	3	0	0	0	4
		18	5	0	0	0	5
		8	0	0	0	0	6
		18	2	0	0	0	7
		12	5	0	0	0	8
		31	1	0	0	0	9
		SEEDED	0	209	7	0	1
			0	10	3	0	2
			2	0	0	0	3
			0	0	0	0	4
			0	0	0	0	5
			0	0	0	0	6
			1	0	0	0	7
			0	0	0	0	8
			10	0	0	0	9
			SEEDED	708	17	2	1
				562	1	1	2
				0	0	0	3
				37	1	0	4
				3	0	0	5
				1	0	0	6
				0	0	0	7
				0	0	0	8
				0	0	0	9
				SEEDED	58	4	1
					135	4	2
					0	0	3
					0	0	4
					2	0	5
					1	0	6
					0	0	7
					7	0	8
					1	0	9

Table 9. Germination of schinus seeds introduced in 1979 to 8 plant communities. On each of the 5 seed-introduction dates, 2,400 seeds were placed in each plot, 800 at each of 3 locations. Numbers are seeds that germinated in the interval since the last count.

Jan 11-12	Feb 13	Mar 12	Apr 19	May 17	July 9, 12	Aug 13, 15	Ecosystem
SEEDED	37	25	0	5	1	0	pineland
	16	20	4	6	0	0	glade
	33	0	0	0	0	0	hammock
	230	43	0	0	0	0	old schinus forest no. 1
	59	4	0	0	0	0	*Myrica*-schinus woodland
	167	33	0	0	0	0	young schinus woodland
	10	2	0	0	0	0	1973 succession
	153	37	44	0	0	0	area bulldozed 1978
	SEEDED	16	0	1	1	0	pineland
		9	5	0	0	0	glade
		4	0	0	0	0	hammock
		7	0	0	0	0	old schinus forest no. 1
		4	1	0	0	0	*Myrica*-schinus woodland
		70	2	1	0	0	young schinus woodland
		1	1	0	0	0	1973 succession
		7	4	0	0	0	area bulldozed 1978
		SEEDED	7	3	0	0	pineland
			11	0	0	0	glade
			0	0	0	0	hammock
			0	0	0	0	old schinus forest no. 1
			0	0	0	0	*Myrica*-schinus woodland
			0	0	0	0	young schinus woodland
			0	0	0	0	1973 succession
			0	1	0	0	area bulldozed 1978
			SEEDED	31	1	0	pineland
				2	0	3	glade
				14	0	0	hammock
				0	0	0	old schinus forest no. 1
				0	0	0	*Myrica*-schinus woodland
				3	0	0	young schinus woodland
				1	0	0	1973 succession
				0	0	0	area bulldozed 1978
				SEEDED	40	0	pineland
					157	4	glade
					2	0	hammock
					2	0	old schinus forest no. 1
					9	0	*Myrica*-schinus woodland
					129	0	young schinus woodland
					15	13	1973 succession
					116	80	area bulldozed 1978

schinus seed germination on these dry sites, but had the opposite effect in lower areas.

The results of the 1980 seed-introduction experiment, in which schinus seedlings were not removed after counting, are summarized in Table 10. As in 1979, seed germination was greatest early in the year (January-February), and was higher immediately following seed introduction than in the months thereafter. Seeds germinated on all sites, but seedling survival was much better on some sites than others (Fig. 23). On 6 sites <1% of the introduced seeds produced seedlings that survived until October, 1980; on 2 sites (both early successional) 1 to 2% of the introduced seeds produced seedlings that survived until October, 1980; and on 1 site (one of the 1975-succession plots) nearly 5% of the introduced seeds produced seedlings that survived until October, 1980. This last-mentioned site is obviously very susceptible to schinus colonization, and in fact has been heavily invaded by schinus. Thus, successful schinus invasion is not only a function of seed access, but also a function of the ability of introduced seeds to germinate, followed by survival of the seedlings. Of the 3 mature ecosystems included in the seed introduction study, the pineland proved to be the most susceptible and the hammock the least susceptible to invasion.

Seedling Transplants

Survival of outplanted schinus seedlings was extremely good at all 10 sites, and survival was not closely related to date of outplanting (Fig. 24). Some outplanted seedlings apparently drowned on the wettest sites (old schinus forest no. 2 and 1975 succession) immediately after the September outplanting, but these seedlings were planted with their tops beneath the water surface. Even on these extremely wet sites survival of the seedlings outplanted in September was 30 to 50%, and survival of seedlings outplanted in other months (July, August, October, November) was higher. Seedlings outplanted into pineland were burned in a prescribed fire in November, 1979, but many resprouted; 8 months later about 20% of the seedlings originally outplanted were still alive.

When the study was terminated, in August, 1980, more than 50% of the outplanted seedlings were still alive on 8 of the 10 sites, and on 4 of the sites fewer than 5 of the 48 outplanted seedlings had died after having been in the field for as long as 2 yr (Fig. 25). Once past the initial germination and establishment phases of growth, schinus seedlings are able to survive on a broad array of sites.

Although seedling survival was good at all sites, there were important differences in the growth rates of outplanted seedlings among the 10 sites (Figs. 26 and 27). On some sites, outplanted seedlings increased 6- to 10- fold in height in the 2 yr following outplanting. Fast seedling growth was characteristic of the 1975 succession (where some trees were >2 m tall and reproductively active when the study was terminated) and the 1973 succession. Seedlings planted in the _Myrica_ woodland also grew very rapidly, even though it had been anticipated that these seedlings would grow slowly (as naturally established seedlings do in that stand) due to allelopathy of _Myrica_ on schinus. The seedlings planted in the _Myrica_ woodland may have benefitted from the plug of marl soil attached to the roots at the time of outplanting.

Table 10. Schinus seed germination and seedling survival resulting from seed introduction in 1980 into 9 plant communities. On each of the 3 seed-introduction dates, 3,000 seeds were placed in each community, 1,000 at each of 3 locations. Numbers are live seedlings on date of count.

Jan 24	Feb 26-27	Apr 3-4	May 5-6	June 5,6,9	Jul 3	Aug 6	Sep 5	Oct 1	Ecosystem
SEEDED	39	44	49	43	44	31	46	45	pineland
	7	9	9	7	3	7	4	5	glade
	6	1	0	0	0	0	0	0	hammock
	42	33	37	32	29	30	28	23	1973 succession
	86	93	96	87	102	101	101	106	1975 succession, plot 1
	285	311	323	316	322	313	318	310	1975 succession, plot 2
	39	44	32	38	41	38	37	27	1975 succession, plot 3
	222	234	228	232	49	10	4	7	area bulldozed 1978
	163	187	205	227	229	274	204	104	area bulldozed 1979
	SEEDED	1	17	21	23	16	15	8	pineland
		13	22	21	20	25	21	20	glade
		0	0	0	0	0	0	0	hammock
		1	1	1	1	1	1	1	1973 succession
		0	19	26	25	17	18	19	1975 succession, plot 1
		7	53	54	76	69	71	71	1975 succession, plot 2
		59	29	18	2	0	0	0	1975 succession, plot 3
		65	82	62	44	29	20	27	area bulldozed 1978
		5	11	12	22	26	25	16	area bulldozed 1979
		SEEDED	0	2	2	1	1	1	pineland
			5	12	4	8	5	6	glade
			0	0	0	0	0	0	hammock
			0	2	1	0	3	1	1973 succession
			104	90	84	69	52	45	1975 succession, plot 1
			72	77	89	68	75	67	1975 succession, plot 2
			1	1	0	1	1	1	1975 succession, plot 3
			14	16	8	0	2	1	area bulldozed 1978
			14	16	14	7	5	4	area bulldozed 1979

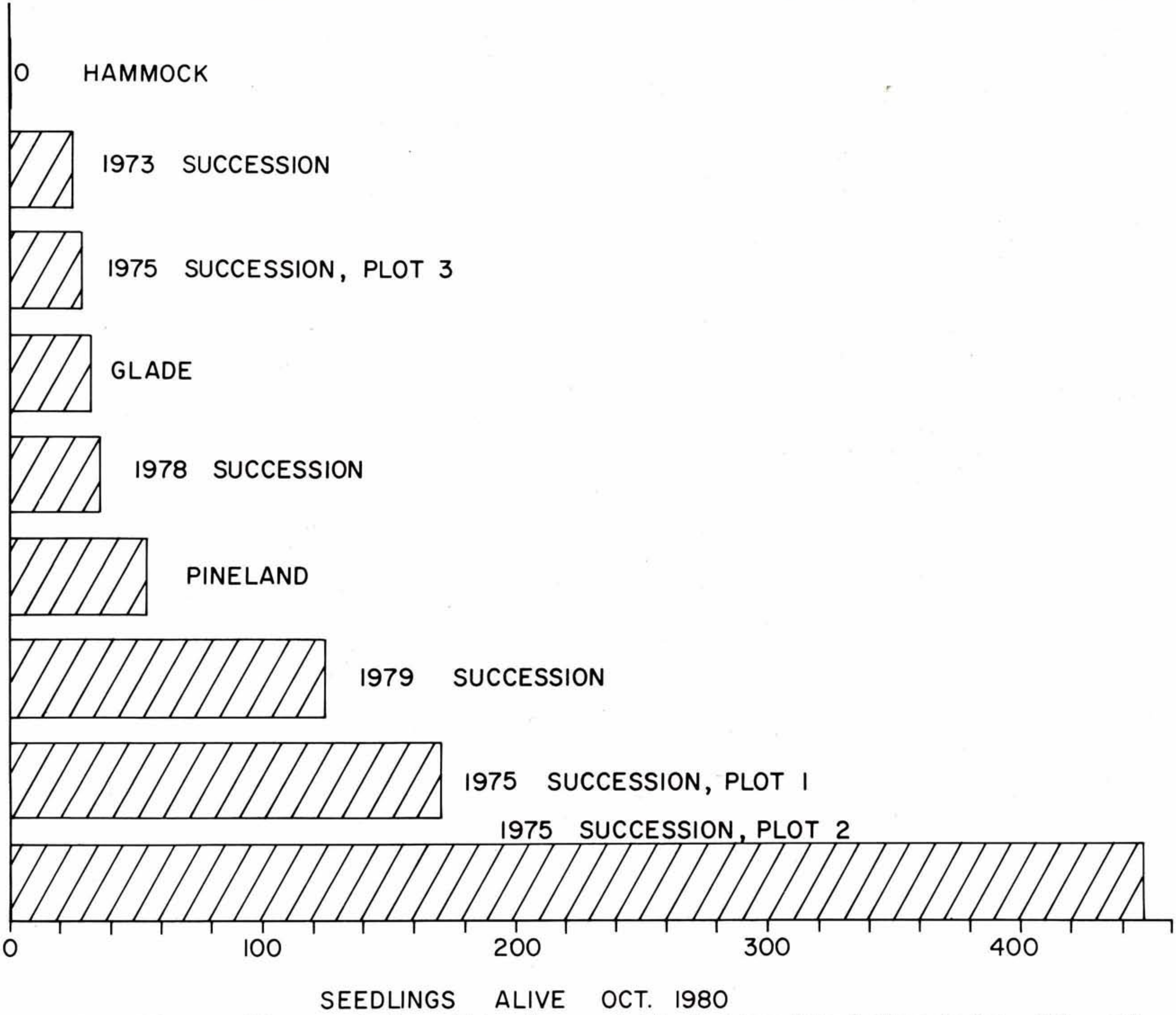


Fig. 23. Schinus seedling survival resulting from seed introductions into 9 sites in Jan., Feb., and April, 1980. The 1978 and 1979 succession sites resulted from bulldozing.

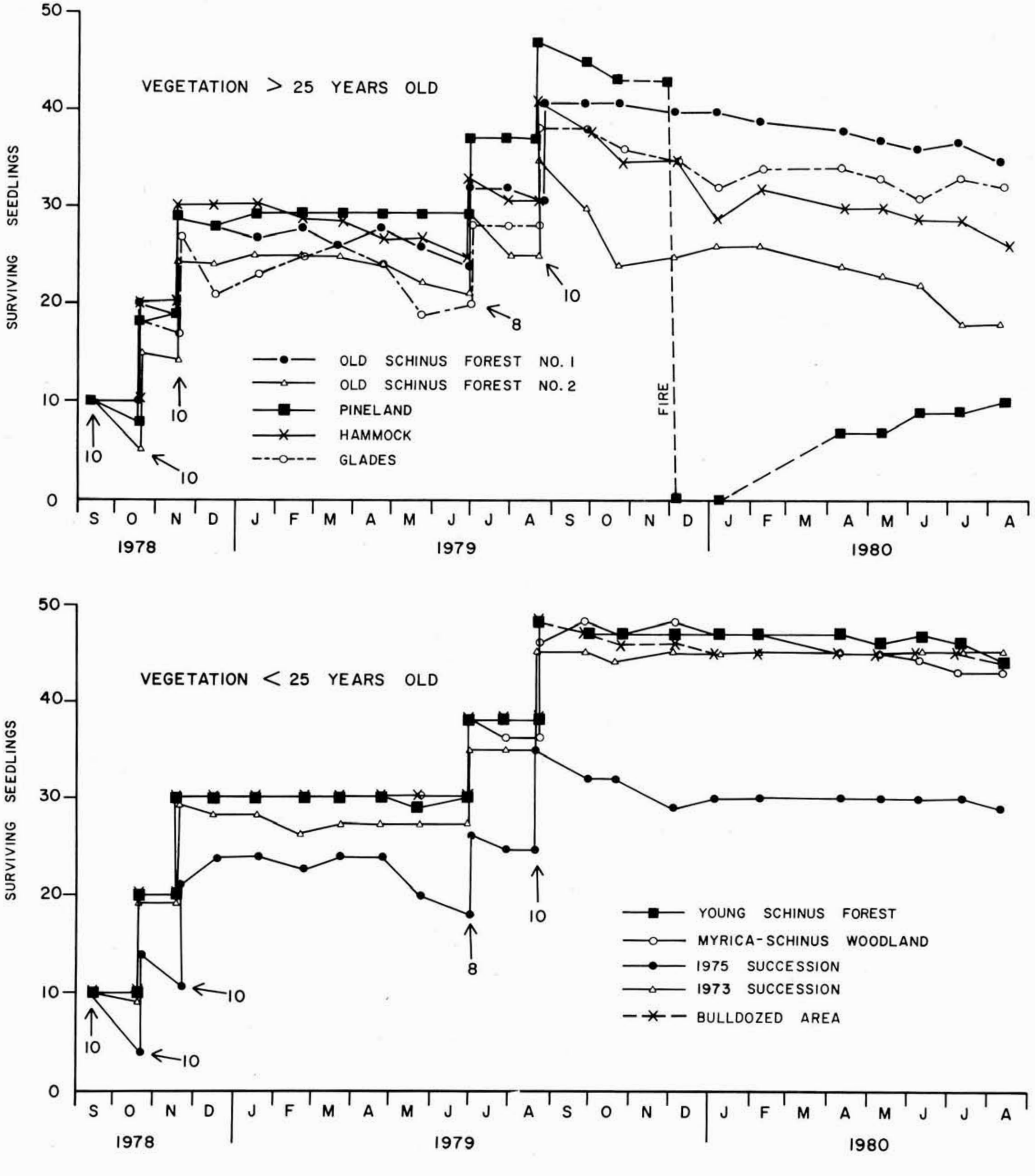


Fig. 24. Survival of schinus seedlings transplanted into 10 sites at 5 times. Numbers and arrows show number (8 or 10) and time of transplants.

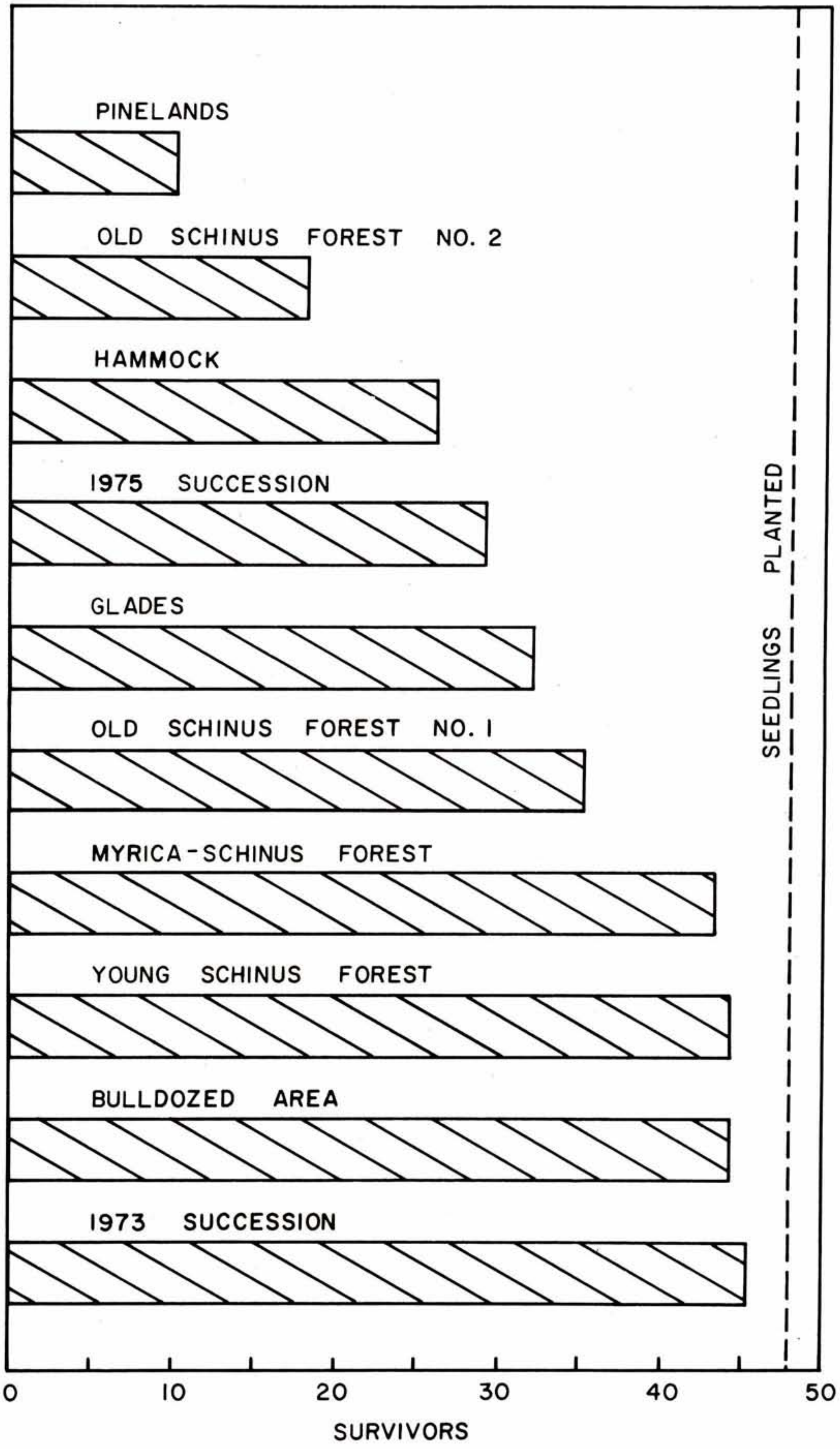


Fig. 25. Survival of transplanted schinus seedlings, through August, 1980.

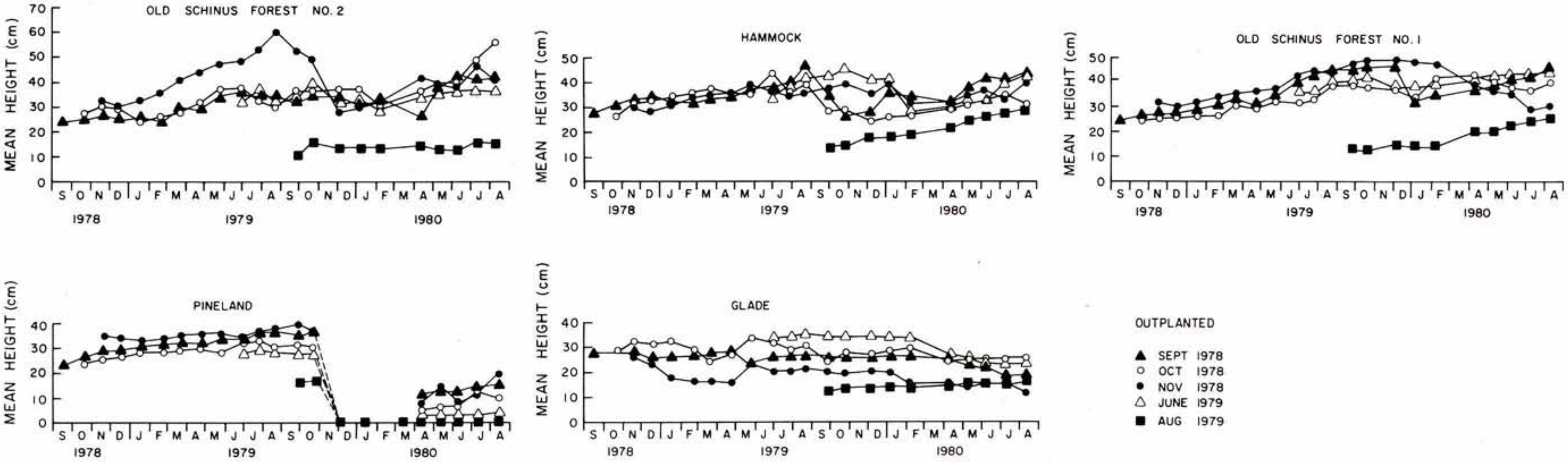


Fig. 26. Height growth of schinus seedlings transplanted into 5 mature or old successional ecosystems.

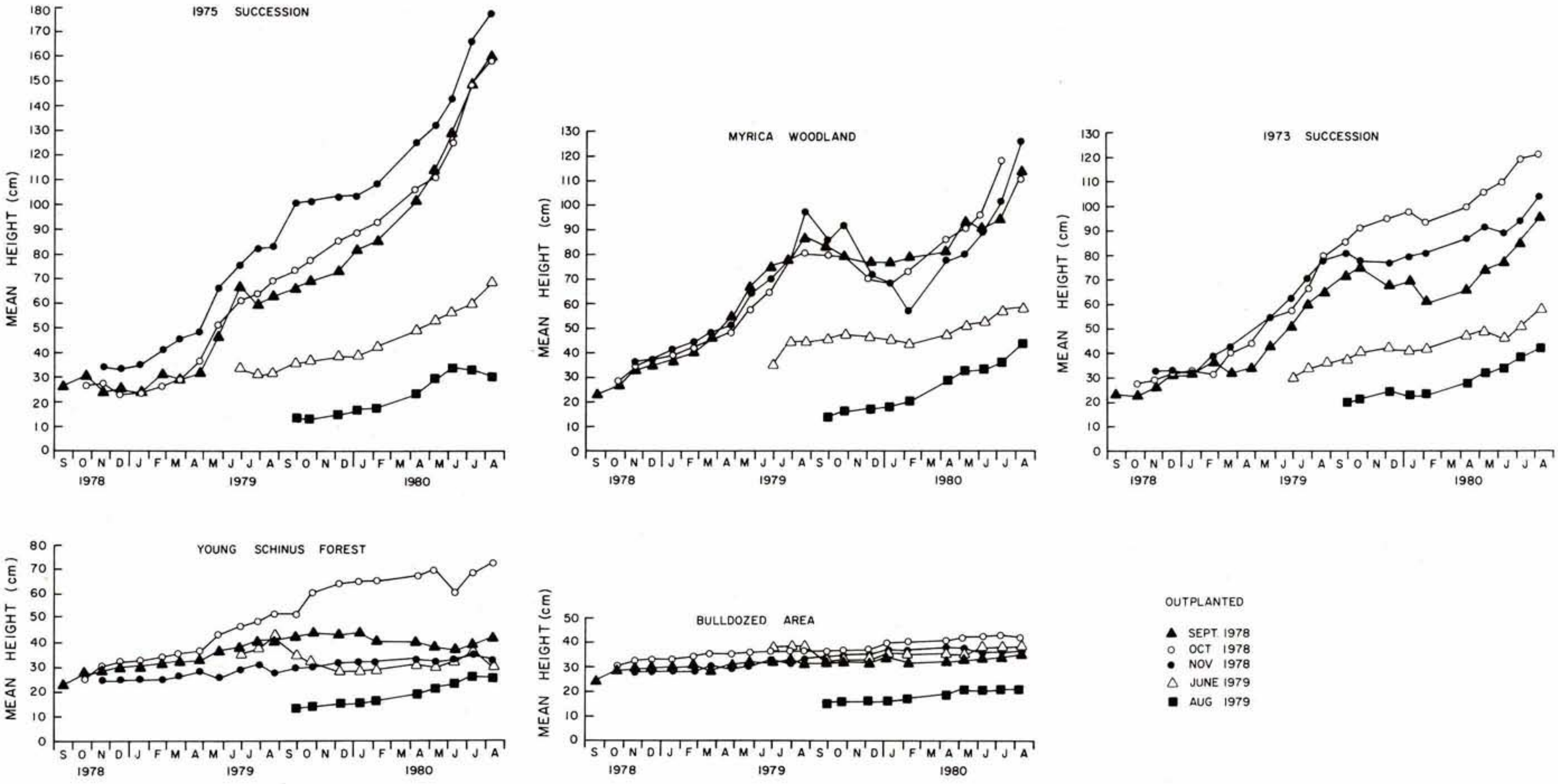


Fig. 27. Height growth of schinus seedlings transplanted into successional ecosystems.

Seedlings outplanted into sites occupied by mature vegetation or by old schinus forests grew slowly, as did seedlings planted on the site that was bulldozed in 1978. In the glade mean seedling height decreased, even though survival there was >50%. Seedlings outplanted into ecosystems that do not presently contain schinus exhibit the same characteristics as naturally occurring seedlings in schinus-dominated vegetation: high survivorship; extremely rapid growth rates in young successional vegetation; and slow growth on poor sites, in dense vegetation, and in mature ecosystems. The 2 exceptions to these generalizations are the slow growth of outplanted seedlings in the bulldozed area, and the rapid growth of seedlings outplanted in the *Myrica* woodland.

SCHINUS FOREST STRUCTURE

Methods

To evaluate schinus abundance and distribution patterns in schinus-dominated regrowth, schinus trees were inventoried in 5 communities: 2 old schinus forests, a *Myrica*-schinus woodland on former pineland, a young schinus woodland, and a site last cleared in 1973. In the 2 old schinus forests and the *Myrica*-schinus woodland the inventory was done on 20 contiguous plots, each 10 by 50 m, for a total sample area of 1 ha per site. In the 2 younger vegetations the inventory was done on 50 plots, each 10 by 10 m, located in a continuous band around the inside perimeter (plus a few plots located in a band across the middle) of a 50 by 200 m rectangle, for a total sample area of 0.5 ha per site.

Because schinus is multiple-stemmed, the schinus inventory on each plot consisted of recording: the number of trees >1 m tall but < 2 cm in diameter; the number of individual trees >2 cm in diameter (at 1.5 m, = DBH); the number of stems ≥2 <10 cm DBH per individual; and the number of stems ≥10 cm DBH per individual.

The coefficient of dispersion was calculated as the ratio of the variance to the mean number of stems per inventory plot.

Results

Schinus stands contain anywhere from about 200 to >2500 schinus trees per ha, comprised of about 600 to >3000 stems (Table 11). Each schinus tree has an average of 2 stems (range of site means = 1.2 to 7.6), most of which are <10 cm DBH. The distribution of schinus trees within stands is highly clumped, more so in intermediate-aged stands on former pinelands than in older or younger stands on former glades.

There are two ways that the multiple stems characteristic of most large schinus trees originate. Some multiple stems result from sprouting of trees whose tops die back due to frost, drought, or fire. Other multiple stemmed trees result from the germination of more than one schinus fruit at the same point. This occurs when schinus infrutecences are dispersed (usually by gravity) before individual fruits are dispersed therefrom, or when schinus seeds germinate in animal stools. Trees containing multiple stems originating from more than one seed frequently

Table 11. Schinus in schinus-dominated regrowth. Sample size was 50, 10 x 10 m plots in young schinus woodland and 1973 succession, and 20, 50 x 10 m plots on other sites. Coefficient of dispersion is ratio of variance to mean number of individuals per plot; values >1 indicate clumped distribution of individuals.

	Old schinus forest no. 1	Old schinus forest no. 2	*Myrica*-schinus woodland	Young schinus woodland	1973 succession
Density (no. per ha)					
Individuals	197	677	354	2,534	292
Branches ≥2 cm diameter	1,496	2,416	596	3,034	676
Branches ≥10 cm diameter	149	102	9	1	14
Stems per tree					
No. ≥2 cm diameter	7.6	3.4	1.7	1.2	2.3
No. ≥10 cm diameter	1.5	1.0	0.1	0.0	0.0
Coefficient of Dispersion	3.6	3.0	10.6	8.1	2.9

have main branches of different sexes, but single-sex individuals are more common, indicating that dieback and resprouting do occur.

Open-growth schinus trees form dome-shaped crowns and their foliage extends to the ground. In closed stands, however, the foliage is concentrated at the top of the canopy (about 10 m tall), and the understory is sparse. Passage is difficult because the abundant schinus stems form a nearly impenetrable tangle. The understory includes various ferns, and the exotic shrub *Ardisia solanacea* is quite common on at least one former glade site. Other tree species besides schinus that reach the canopy include *Myrsine floridana*, *Persea borbonia*, *Ilex cassine*, *Nectandra coriacea*, and the exotic *Psidium guajava*. On former pine sites *Myrica cerifera* is a dominant tree: sometimes more abundant than schinus.

Old schinus stands are not monospecific, even though they are dominated by schinus. Native species invade successfully, and clumps of native trees are common. The life span of schinus in South Florida is not known, but in some of the older stands studied (>35 yr old) the larger schinus were continually falling and dying, and multiple-stemmed clumps were breaking up. However, because of the shade tolerance of schinus seedlings, and the rapid growth of these understory seedlings once released, old schinus forests continue to be dominated by schinus even after the canopy trees die. This represents an unusual instance of an aggressive, weedy species that is capable of reproducing in its own shade and maintaining its dominance on a site for more than one generation. The future successional changes that may occur in these old schinus dominated forests are unknown.

HERBICIDE EVALUATIONS

Properly applied herbicides offer promise as one way to contain schinus. In most agricultural situations where herbicides are used, they are directed at many species, and there is a single non-target species: the crop. Furthermore, long-lasting control of target species, perhaps through retention of the herbicide in the soil, is often desirable. In a national park, however, the situation is the opposite. There is a single target--schinus in this case--and everything else in a non-target species. Also, herbicide persistence in the soil is undesirable both because of its potential long-term environmental implications and because it might inhibit the regrowth of native vegetation. Herbicides, because of the ways they affect the physiology of plants, are less specific than some other kinds of pesticides; broad-spectrum action is the rule rather than the exception with herbicides.

Against this background of: the need to attack a single target species; the need to disrupt the native vegetation as little as possible and for the shortest time possible; the special concern for long-term environmental protection; and the knowledge that no chemical was specific to the target species, experiments were conducted to test the effectiveness of various herbicides for schinus control.

Methods

Herbicides were screened before being chosen for testing. Three groups of herbicides were eliminated: 1) those banned for use in national parks by the Department of the Interior, 2) those known to be either very mobile or very persistent in the soil (as documented, for example, in WSSA, 1979), and 3) those previously demonstrated to be ineffective against schinus (e.g. by Woodall, 1979b). Classes of herbicides eliminated on these grounds included salts, organic arsenicals, dipyridiliums, phenoxys, uracils, and ureas.

After this initial screening 5 herbicides were chosen for field trials. These were: a dicamba + 2,4-D combination; granular dicamba; an isopropylamine salt of glyphosate; a triazine compound; and an ester formulation of triclopyr. The herbicides, formulations, and concentrations applied are summarized in Table 12. All dosages used fell within the ranges recommended on the labels supplied by the manufacturers. Liquid foliar applications were made using hand-pumped, back-pack sprayers, and the crowns were sprayed until thoroughly wetted and drip was observed. The invert formulation of dicamba + 2,4-D had the consistency of dilute mayonnaise, and was applied to foliage with a special emulsion-forming pump. Two formulations were applied topically to the bark using back-pack sprayers, and each trunk was wetted around its complete circumference; the bark was not cut and the chemical was not injected. Granular herbicides were scattered uniformly on the soil beneath the target tree, within the drip line of the crown.

There were 15 treatments--the 14 listed in Table 12 plus controls--and each treatment was randomly assigned to 13 schinus trees. The heights of the 195 target trees ranged from about 1 to 5 m, with a mean ± standard deviation of 2.4 ± 0.7 m. Of these, 146 were located on former pineland northwest of the Research Center and 49 were in former pineland east of the Scout Camp. The sex of 166 (85%) of the target trees was known: 91 (55%) were females and 75 (45%) were males.

Herbicides were applied in February and March for 2 reasons. First, low water levels increase site accessibility and eliminate the environmental hazards associated with introducing herbicides to flooded soil. Second, herbicide uptake is greatest if applied when a plant is metabolically active or, in the case of schinus, producing new leaves. Male trees produced new leaves after the end of autumn flowering in November. Female trees, however, do not resume new leaf production until fruit fall is completed in February-March. (See section on PHENOLOGY).

All treated trees were monitored approximately 2 and 4 weeks after treatment, then again in June, July and November. The trees treated in February were monitored a sixth time, in April. The researcher assessing the responses of target trees and surrounding vegetation did not know which treatment had been applied to which tree. The final observation (Nov., 1980) included field examination of target-tree cambium to distiinguish between dead trunks and those that were defoliated, but still alive.

Table 12. Herbicide concentrations applied. Each of the 14 formulations was applied to 13 randomly assigned schinus. All applications were in 1980.

Common name	Product name	Form applied	Applied to	Date applied	Concentration or amount
dicamba + 2,4-D	Banvel 720[a]	liquid	foliage	6-7 Feb	50 ml $\cdot$ l^{-1} H_2O
				6 Feb	25 ml $\cdot$ l^{-1} H_2O
dicamba + 2,4-D	Banvel 720[a]	invert	foliage	6 Feb	50 ml $\cdot$ (1000 ml H_2O + 330 ml diesel + 83 ml adjuvant)$^{-1}$
				11 Feb	25 ml $\cdot$ (1000 ml H_2O + 330 ml diesel + 83 ml adjuvant)$^{-1}$
dicamba	Banvel 5G[a]	granular	soil	13 Feb	48 ml $\cdot$ m^{-1} crown diameter
				13 Feb	8 ml $\cdot$ m^{-1} crown diameter
glyphosate	Roundup[b]	liquid	foliage	12 Feb	17 ml $\cdot$ l^{-1} H_2O
				12 Feb	8 ml $\cdot$ l^{-1} H_2O
triclopyr	Garlon (M-4021)[c]	liquid	bark	26 March	15 ml $\cdot$ l^{-1} diesel
				26 March	5 ml $\cdot$ l^{-1} diesel
triclopyr	Garlon (M-4021)[c]	liquid	foliage	12 Feb	8 ml $\cdot$ l^{-1} H_2O
				12 Feb	3 ml $\cdot$ l^{-1} H_2O
(none assigned)	Velpar[d]	liquid	foliage	13 Feb	24 g $\cdot$ l^{-1} H_2O
				12 Feb	12 g $\cdot$ l^{-1} H_2O

---

[a] Velsicol Chemical Corporation

[b] Monsanto Agricultural Products Company

[c] Dow Chemical Company

[d] E. I. duPont de Nemours & Company

Each target tree was monitored with respect to 8 variables evaluated over the entire tree, and scored on a 3-point scale:

1 = 0 to 24% (little damage)
2 = 25 to 75%
3 = 76 to 100% (severe damage)

The 8 responses recorded were:

CURL - leaf wilting and revoluted margins.

SPOT - discontinuous discoloration on leaf surface.

BURN - 100% browning or blackening of both leaf surfaces (thus BURN and SPOT damage were mutually exclusive on a single leaf, but one tree could bear leaves of both symptoms).

DROP - leaflet fall, whether or not rachis was retained.

FRUIT - presence or absence of fruits on female trees.

SPROUT - the number of new sprouts (counted up to 50 and recorded as >50 when more were present), subdivided into 2 categories: 1) those above the root collar, including normal flushing, and 2) those below the root collar, including basal sprouts and when traceable, root suckers.

VIGOR - a qualitative rank referring to the general health and appearance of the sample tree. It was recorded on a 3-point scale:

1 = Good	normal growth; flowering and/or flushing; no chlorosis; had to have 4 class-1 leaf ratings (CURL, SPOT, BURN, DROP, as described above) or no worse than 3 class-1 and 1 class-2 ratings; could not have any class-3 ratings.
2 = Average	no more than 2 class-2 ratings; trees that had 3 class-1 ratings but were uniformly chlorotic received a VIGOR rating of 2.
3 = Poor	tree had one or more of the following symptoms: bark fissures, substantial sap exudation, fungus- or insect-caused disease, severe chlorosis, 1 class-3 rating, or ≥ 2 class-2 leaf rating.

The impact of herbicides on the surrounding vegetation was also of interest, so nearby shrubs and understory vegetation were monitored. The two shrubs (>1.0 m tall) nearest each target tree were tagged and injury to them was recorded in much the same way as injury to target trees. Two sets of observations were recorded for each neighboring shrub: 1 for half of the crown facing toward the target tree and the other for the half of the crown facing away from the target tree. In a few cases there were no nearest shrubs (because of proximity to another treated schinus tree), in a few cases there was only 1 nearest shrub, and sometimes (e.g., when a vine was found growing among the branches of a target tree) the response of 3 or more nearest-neighbors was monitored. When the nearest neighbor was beyond the range of maximum anticipated herbicide drift (about 10 m), it was not monitored. The nearest-neighbor shrubs were comprised of 14 species, of which 5 accounted for 96% of the 331 individuals monitored. These 5 included 2 exotics: schinus (20.5% of the individuals) and Psidium guajava (3.3%); and 3 native species: Baccharis halimifolia, including some B. glomeruliflora (61.0%), Myrica cerifera (8.5%), and Dodonaea viscosa (2.7%).

The impact of herbicides on the understory vegetation (<1 m tall) within the drip-line of each target tree was also monitored. The foliage was scored with respect to CURL, SPOT, and BURN, and given a general VIGOR ranking, as described above. The response of the common composite herb, Bidens alba, was not recorded because it was not possible to distinguish between herbicide-related damage and the natural tendency of this species to retain dead, shriveled leaves.

Results

Schinus responded quickly to herbicide applications (Tables 13 through 16). The effects of all formulations tested were visible within 2 wk after application, except in the case of the granular form of dicamba applied to the soil. The granular-dicamba effects were not readily apparent until at least 2 mo after application, and this herbicide did not prove very effective at killing schinus, even after 9 mo following application. Malformed epicormic and basal sprouts were observed after defoliation following application of dicamba + 2,4-D (low and high doses of both aqueous and invert formulations) and Velpar (low dose), but most of these sprouts later died.

A measure of great interest is target-tree mortality (Fig. 28). Schinus kill >90% was achieved with the high dose of triclopyr applied to foliage, the high dose of glyphosate, high and low doses of triclopyr applied to bark, and high and low doses of Velpar. Thus, triclopyr, glyphosate, and Velpar all proved to be effective at killing schinus.

The impact of the test herbicides on neighboring shrubs and vines (both native species and exotics) was different from the effects of these chemicals on target trees (Fig. 29). Of the 3 chemicals that were effective in killing schinus, only the high and low doses of triclopyr to the bark of target trees resulted in 50% mortality of neighboring shrubs and vines. This reflects the very local application of the chemical to the basal bark, which results in very little herbicide drift to nearby plants. Both high and low dosages of Velpar killed >75% of neighboring shrubs and vines.

Herbicide impact on the understory vegetation is extremely important if native plants are to capture the gaps created by the death of mature schinus trees before such gaps can be recolonized by new schinus. In most cases, understory vegetation showed signs of recovery within 5 mo after herbicide application (Table 17). An important exception was

Table 13. Time course of target-tree leaf wilting after herbicide application. Wilting was defined as >75% of leaves curled, having revolute margins, or having drooping rachises. Values are per cent of sample trees, but only those that were not completely defoliated at the time of observation. DEF = 100% defoliation. ND = no data.

	Mean days post-treatment (Range)					
Treatment	13 (9-16)	27 (27-35)	77 (77-84)	121 (121-128)	167* (167-174)	268 (265-272)
control	0	0	0	15	8	8
glyphosate, low	62	57	75	DEF	DEF	DEF
glyphosate, high	62	100	100	DEF	DEF	DEF
dicamba + 2,4-D, liquid, low	69	100	100	DEF	DEF	DEF
dicamba + 2,4-D, liquid, high	92	100	100	DEF	DEF	DEF
dicamba + 2,4-D, invert, low	100	100	100	DEF	DEF	DEF
dicamba + 2,4-D, invert, high	92	100	100	DEF	DEF	DEF
dicamba, granular, low	8	8	0	58	58	45
dicamba, granular, high	0	0	25	62	50	71
triclopyr, bark, low	91	100	DEF	DEF	DEF	ND
triclopyr, bark, high	77	100	DEF	DEF	DEF	ND
triclopyr, foliar, low	100	100	DEF	DEF	DEF	ND
triclopyr, foliar, high	100	100	DEF	DEF	DEF	ND
Velpar, low	0	75	DEF	DEF	DEF	DEF
Velpar, high	23	43	DEF	DEF	DEF	DEF

* Does not include triclopyr treatments, which received fifth, and final observation 222 days after application.

Table 14. Time course of target-tree leaf discoloration after herbicide application. Discoloration was defined as >75% of leaves being mottled or chlorotic. Values are per cent of sample trees, but only those that were not completely defoliated at the time of observation. DEF = 100% defoliation. ND = no data.

	Mean days post-treatment (Range)					
Treatment	13 (9-16)	27 (27-35)	77 (77-84)	121 (121-128)	167* (167-174)	268 (265-272)
control	0	0	15	0	0	0
glyphosate, low	23	0	0	DEF	DEF	DEF
glyphosate, high	23	0	0	DEF	DEF	DEF
dicamba + 2,4-D, liquid, low	38	0	0	DEF	DEF	DEF
dicamba + 2,4-D, liquid, high	62	0	0	DEF	DEF	DEF
dicamba + 2,4-D, invert, low	8	0	0	DEF	DEF	DEF
dicamba + 2,4-D, invert, high	0	0	0	DEF	DEF	DEF
dicamba, granular, low	8	8	8	0	0	9
dicamba, granular, high	0	0	8	0	38	0
triclopyr, bark, low	0	0	DEF	DEF	DEF	ND
triclopyr, bark, high	23	0	DEF	DEF	DEF	ND
triclopyr, foliar, low	0	0	DEF	DEF	DEF	ND
triclopyr, foliar, high	0	0	DEF	DEF	DEF	ND
Velpar, low	23	0	DEF	DEF	DEF	DEF
Velpar, high	15	43	DEF	DEF	DEF	DEF

* Does not include triclopyr treatments, which received fifth, and final observation 222 days after application.

Table 15. Time course of target-tree leaf burn after herbicide application. Leaf burn was defined as >75% of leaves being uniformly brown or black. Values are per cent of sample trees, but only those that were not completely defoliated at the time of observation. DEF = 100% defoliation. ND = no data.

	Mean days post-treatment (Range)					
Treatment	13 (9-16)	27 (27-35)	77 (77-84)	121 (121-128)	167* (167-174)	268 (265-272)
control	0	0	0	0	0	0
glyphosate, low	31	57	75	DEF	DEF	DEF
glyphosate, high	38	100	100	DEF	DEF	DEF
dicamba + 2,4-D, liquid, low	62	100	100	100	DEF	DEF
dicamba + 2,4-D, liquid, high	77	100	100	100	DEF	DEF
dicamba + 2,4-D, invert, low	100	100	100	100	DEF	DEF
dicamba + 2,4-D, invert, high	100	100	100	100	DEF	DEF
dicamba, granular, low	0	8	0	0	0	0
dicamba, granular, high	0	0	8	0	0	0
triclopyr, bark, low	54	100	100	DEF	DEF	ND
triclopyr, bark, high	38	100	100	DEF	DEF	ND
triclopyr, foliar, low	92	100	67	DEF	DEF	ND
triclopyr, foliar, high	92	100	100	DEF	DEF	ND
Velpar, low	0	25	DEF	DEF	DEF	DEF
Velpar, high	0	29	DEF	DEF	DEF	DEF

* Does not include triclopyr treatments, which received fifth, and final observation 222 days after application.

Table 16. Time course of target-tree defoliation after herbicide application. Defoliation was defined as > 75% leaf loss. Values are per cent of sample trees. ND = no data.

	Mean days post-treatment (Range)					
Treatment	13 (9-16)	27 (27-35)	77 (77-84)	121 (121-128)	167* (167-174)	268 (265-272)
control	0	0	0	0	0	0
glyphosate, low	46	85	92	92	77	54
glyphosate, high	23	77	92	100	100	100
dicamba + 2,4-D, liquid, low	0	62	92	100	85	77
dicamba + 2,4-D, liquid, high	0	46	85	100	85	58
dicamba + 2,4-D, invert, low	0	17	77	100	85	62
dicamba + 2,4-D, invert, high	0	17	38	100	77	73
dicamba, granular, low	0	8	8	8	8	8
dicamba, granular, high	0	0	31	38	28	18
triclopyr, bark, low	46	92	100	100	100	ND
triclopyr, bark, high	0	62	100	100	100	ND
triclopyr, foliar, low	8	62	100	85	77	ND
triclopyr, foliar, high	0	0	100	100	92	ND
Velpar, low	62	100	15	100	100	100
Velpar, high	0	100	23	100	100	100

* Does not include triclopyr treatments, which received fifth, and final observation 222 days after application.

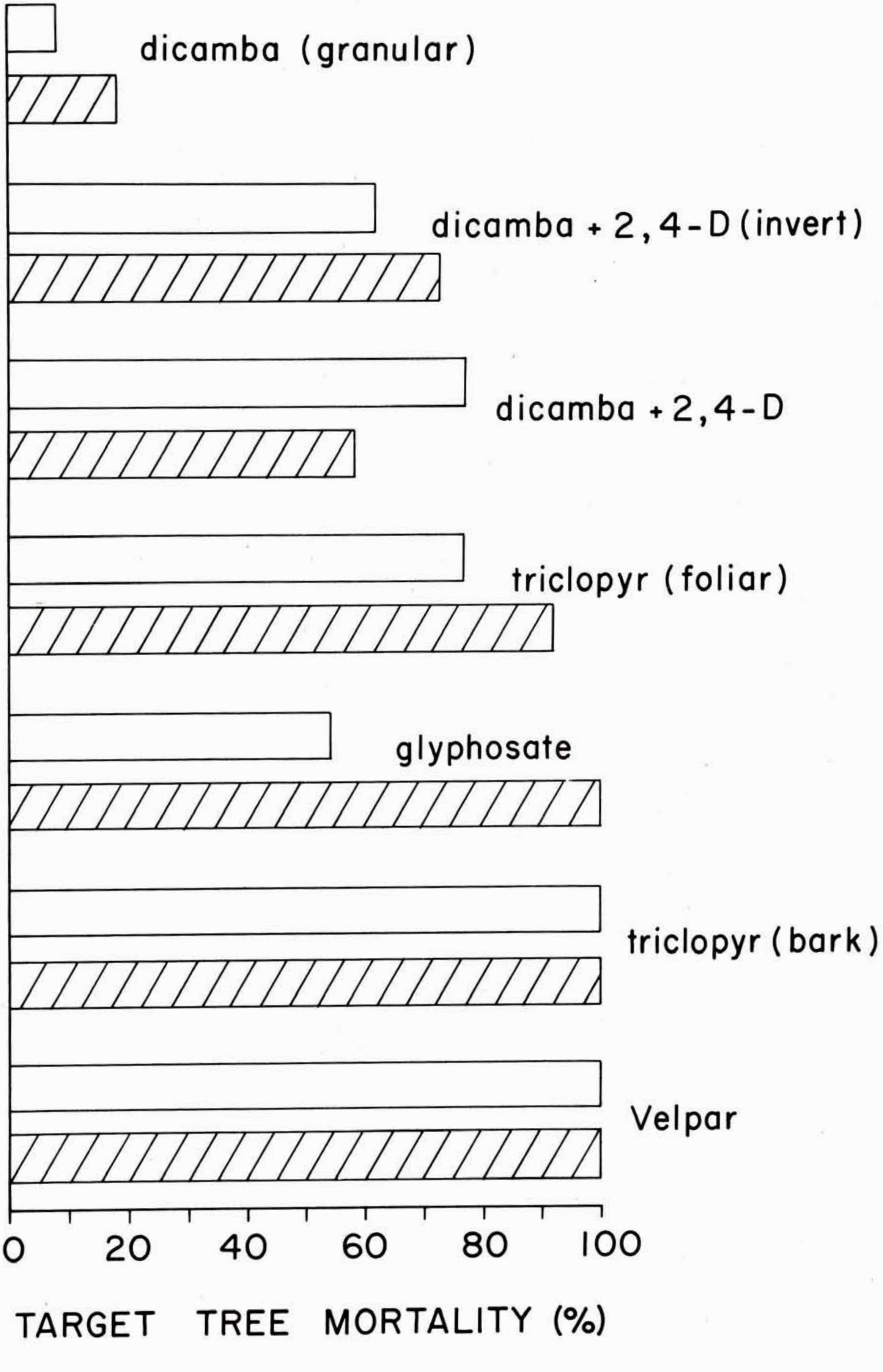


Fig. 28. Effectiveness of 14 herbicide formulations in killing schinus. Cross hatching = high dosage; open bar = low dosage. There was no mortality of control (no treatment) trees.

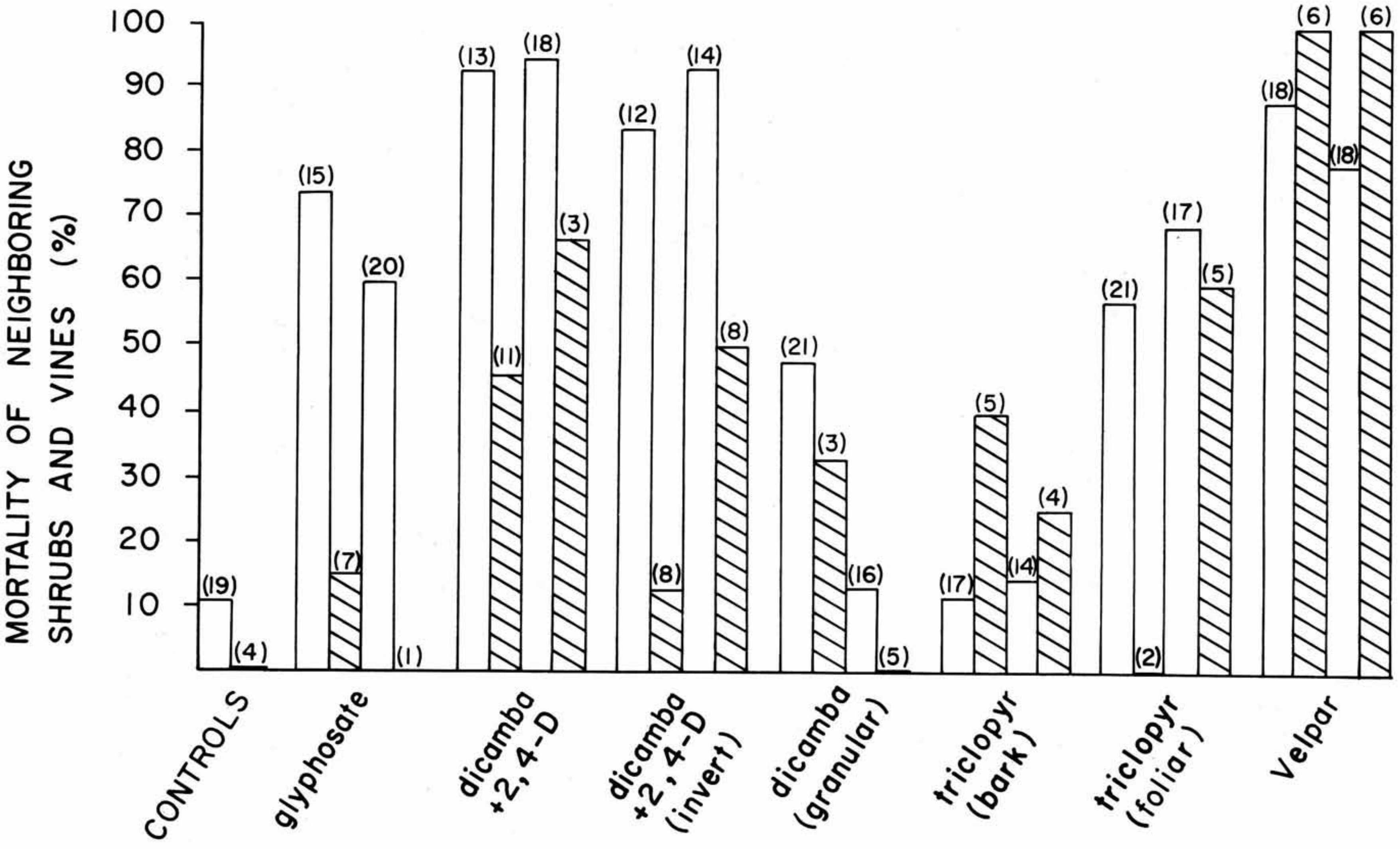


Fig. 29. Herbicide impacts on neighboring shrubs and vines. Number at top of bar is number of individuals monitored. Open bar is native species; cross-hatched bar is exotics. Two left-most bars above each treatment are high dose; two right-most bars are low dose.

Table 17. Time course of herbaceous understory response to herbicide application on overstory schinus trees. Values are per cent of target-tree understories having >75% normal growth. ND = no data.

	Mean days post-treatment (Range)					
Treatment	13 (9-16)	27 (27-35)	77 (77-84)	121 (121-128)	167* (167-174)	268 (265-272)
control	91	83	100	85	92	100
glyphosate, low	62	8	38	15	38	46
glyphosate, high	18	0	55	36	38	58
dicamba + 2,4-D, liquid, low	9	8	55	25	23	54
dicamba + 2,4-D, liquid, high	0	20	60	10	31	50
dicamba + 2,4-D, invert, low	0	0	62	0	15	50
dicamba + 2,4-D, invert, high	0	8	0	0	0	0
dicamba, granular, low	75	42	83	42	77	83
dicamba, granular, high	100	62	62	38	46	82
triclopyr, bark, low	85	62	31	46	91	ND
triclopyr, bark, high	83	50	0	38	92	ND
triclopyr, foliar, low	54	46	0	31	85	ND
triclopyr, foliar, high	8	17	15	31	54	ND
Velpar, low	50	8	0	0	0	0
Velpar, high	33	0	0	0	8	0

* Does not include triclopyr treatments, which received fifth, and final observation 222 days after application.

Velpar; the effects of this herbicide are very long-lasting, and the understory vegetation beneath trees treated with Velpar was mostly dead even 9 mo after application. Triclopyr, especially when applied to the bark, had little long-term impact on understory plants (Fig. 30).

Three kinds of evidence are available for herbicide evaluation: effectiveness in killing target trees; death of nearby shrubs and vines; and impact (severity and duration) on understory vegetation. Dicamba and dicamba + 2,4-D are not as effective in killing schinus as other chemicals tested. Velpar kills schinus, but everything else as well. Where foliar applications are called for (e.g., where large numbers of small individuals are to be killed, as in the understory of a stand), either triclopyr or glyphosate can be recommended. For killing large schinus trees, however, basal application of herbicide may be preferable because the impact on non-target plants is very limited. The only basal application tested (high and low doses of triclopyr) killed 100% of the trees to which they were applied, but other (untested) chemicals may be just as safe and do the job just as well. Based on the findings reported here, the low dose of triclopyr applied in a band completely around each main trunk, seems to be a safe effective way to kill schinus.

STAND CONVERSION

Schinus is an important component of many second-growth forests--both young and old--in the study area, and it may be desirable to reduce the importance of this exotic tree in those stands. This can be accomplished by bulldozing followed by burning the windrowed vegetation. However, such intensive management practices are expensive, and success is not always certain, especially if the burn is incomplete and the bulldozed schinus resprouts. Furthermore, disturbed sites are especially susceptible to schinus invasion. In addition, drastic management techniques such as bulldozing and burning of forests are incompatible with most managers' attitudes toward landscape manipulation in national parks.

As an alternative approach toward schinus forest conversion, we proposed that the slow conversion of schinus-dominated forests to forests dominated by native plants be attempted by killing reproductively mature female schinus trees: a technique we dubbed "matricide". The idea was that the unkilled vegetation, including male schinus trees, would keep the site fully occupied, thus reducing the probability of site recapture by schinus. By killing females the reproductive potential of the undesirable species would be reduced, and the stand might gradually be converted to one consisting mainly of native species.

Methods

To test these ideas on gradual stand conversion, 2 experiments were conducted. One was a pilot study, in which single mature female trees were killed, and the response of understory plants was monitored. The other involved killing all mature females on larger plots.

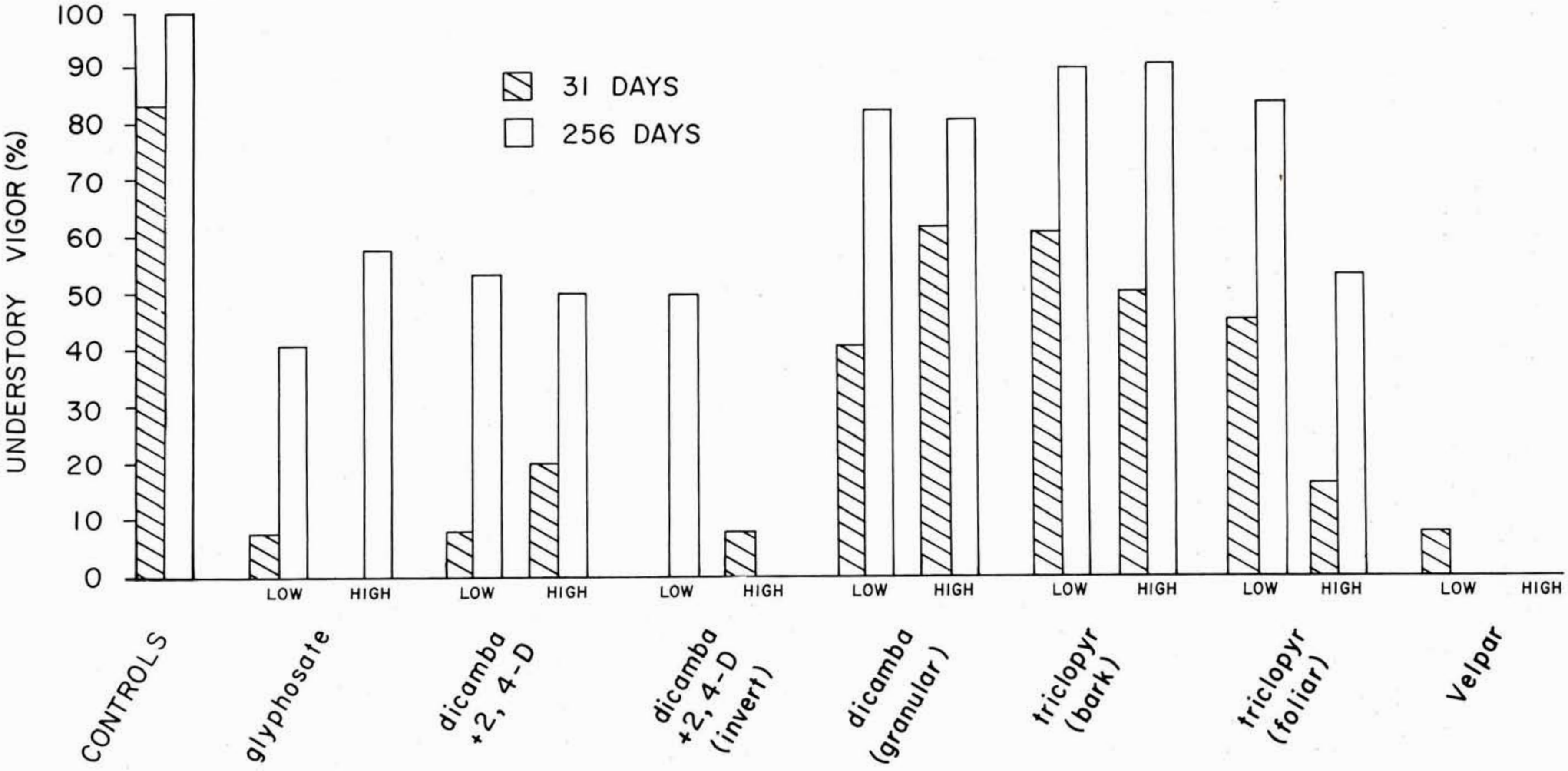


Fig. 30. Herbicide impacts on the vigor of understory vegetation beneath target trees.

Pilot Study

The pilot study was used not only to study possibilities for stand conversion but also to assess the response of understory schinus seedlings to canopy-gap formation. The methods for the pilot study were described earlier, in the last 3 paragraphs of the Methods subsection of the section on SEEDLING GROWTH AND SURVIVORSHIP. In brief, 2 female, canopy schinus trees were selected on each of 4 sites: old schinus forests nos. 1 and 2, and *Myrica*-schinus woodland, and the young schinus forest. Beneath each tree, 4 long, narrow plots (each with a smaller seedling recruitment plot appended to 1 side) were established radiating outward from the base of the schinus trunk. On November 7, 1978, 1 member of each pair of female schinus was randomly selected and killed. The understory vegetation received no treatment because one of the objectives of the pilot study was to monitor the response of understory schinus seedlings to the creation of canopy gaps. Schinus seedling density, germination, and mortality were monitored approximately biweekly, from early 1978 through October 1980.

Larger-scale Study

Promising results obtained from the pilot study led to the establishment of a larger-scale study of stand conversion. One difficulty with the pilot study was that, because only selected canopy females were killed, the gaps created were readily accessible to schinus seed inputs from other, nearby schinus trees. Therefore, in early 1980 larger plots were established in 3 stands, and all females in those plots were killed.

Each plot was 50 by 50 m, and the female schinus trees in an additional 5 m buffer strip around each plot were also killed, for a total treatment area of 3600 m^2 per site. The sites, schinus sizes and density per plot, and dates of herbicide application are summarized in Table 18. Canopy female trees were killed by basal bark application of triclopyr. The understory beneath selected canopy trees was killed by backpack sprayer application of glyphosate, with care taken to concentrate the spray on schinus seedlings and to avoid damage to native plants insofar as possible.

In each plot, 8 schinus trees were chosen: 4 males (scheduled to be left alive) and 4 females (scheduled to be killed). The understory beneath 2 mature schinus of each sex was randomly selected to be killed with herbicide. Half of the trees were randomly chosen to have a diverse mixture of seeds of native species applied to the soil beneath their crown. In summary, the treatments consisted of all 8 of the following combinations: overstory killed or not killed; understory killed or not killed; seeds applied or not applied.

To test the idea that site capture by native species might be enhanced if seeds were applied beneath killed female schinus trees, propagule packages containing seeds of 14 native, woody species were made up (Table 19). In early June, the contents of 1 such propagule package were scattered beneath each of 12 sample trees: 4 per site. A subsample of 200 seeds of each species (only 10 for *Myrsine*, 15 each for *Trema* and *Persea*, and 20 for *Guettarda*) was tested for germination by

Table 18. Schinus density, treatment dates, and sample-tree characteristics in 3, 60 x 60 m plots where mature females were killed. The understory beneath selected female schinus was sprayed with herbicide on 1 April 1980 at all 3 sites.

		Date herbicide applied to canopy trees		
Site	Number of female schinus killed	First application	Second application	Mean (S.D.) crown area of 8 sample trees (m^2)
Old schinus forest no. 1	33	1 Apr 80	23 Apr 80	86.0 (65.3)
Myrica-schinus woodland	10	28 Mar 80	23 Apr 80	86.8 (51.7)
Young schinus forest	81	28 Mar 80	24 Apr 80	39.1 (17.9)

Table 19. Contents of propagule package added beneath mature schinus trees, large-scale matricide. All species were woody, native plants, and were collected in or near the study areas.

No.	Species	Number of seeds applied
1	*Ludwigia* spp.	60,764
2	*Baccharis* spp.	14,387
3	*Myrica cerifera*	10,400
4	*Cephalanthus occidentalis*	2,011
5	*Dodonaea viscosa*	1,504
6	*Callicarpa americana*	1,208
7	*Ilex cassine*	1,157
8	*Rhus copallina*	714
9	*Psychotria ligustrifolia*	350
10	*Tetrazygia bicolor*	42
11	*Guettarda scabra*	25
12	*Trema micrantha*	16
13	*Persea borbonia*	4
14	*Myrsine floridana*	2
	Total	92,584

placing seeds (usually 10 replications of 20 seeds each) on filter paper moistened with distilled water in covered Petri dishes.

Beneath each of the 8 sample trees per plot, a plot was established to monitor understory vegetation. Each plot was 0.5 m by 5 m, and its long axis extended outward from the schinus tree trunk at 1 of 4 randomly selected directions: NE, SE, NW, or SW. These directions were chosen to assure that the sample plots would cross the east-west rows and furrows at 45°. Each plot was divided into 5, 1 m long intervals, and most kinds of data were recorded by interval.

In January (before herbicide application) and again in June, 1980 (after herbicide application) all plants in each plot were identified and counted. Data were recorded by interval within plots, and 3 height classes of plants were distinguished 0-1, 1-3, and >3 m.

Leaf area index (LAI) of both the canopy and the understory was measured in March (just prior to herbicide application), June, and November, 1980. The sampling method consisted of suspending a cord or thin rod vertically through the vegetation and counting the number of leaves intercepted. By this method, in which the horizontal area sampled is assumed to be equal to 0, 1 interception of a leaf equals 1 unit of LAI. Data were recorded by height above the ground (25 cm intervals) and by species.

To measure LAI from the canopy to the forest floor, a cord was suspended down through the canopy foliage from a long extendable pole. The cord was weighted with a plumb bob and controlled vertically with a fishing reel. The cord was marked at 25 cm intervals to facilitate recording of LAI by height. Beneath each sample tree, 2 directions (N, S, E, or W) were randomly chosen. Along the chosen bearings, and 2 m away from the tree trunk, a sample point was established. Around each sample point, 5 bearings (0 to 360°, at 1° intervals) were randomly selected, and the cord was dropped vertically through the vegetation about 1 m away from the sample point in the direction of each bearing chosen. Thus, at the time of each sampling 10 LAI measurements were taken at each sample tree: 5 around each of 2 sample points.

To sample the LAI of ground cover, a slender rod was used. It was placed vertically 5 times in each 1-m interval of the permanent sample plot beneath each tree, for a total sample size of 25 LAI measurements per tree each time. Understory LAI was recorded, by species, from 0 to 25 and 25 to 50 cm above the ground.

Results

Pilot Study

One of the key responses observed after the pilot matricide study, in which selected overstory female schinus trees were killed, was the growth of the schinus seedlings already established on the forest floor. The growth response of these understory schinus seedlings was reported in the section on SEEDLING GROWTH AND SURVIVORSHIP, Fig. 22. In old schinus forest no. 1, the understory schinus seedlings did not respond to canopy-gap formation because the canopy quickly closed due to ingrowth of surrounding trees, mostly male schinus. On the other 3 sites, however, the growth response of the schinus seedlings was dramatic. Schinus seedlings beneath untreated trees grew very little over the 2-yr period of observation, whereas seedlings in gaps more than doubled in height during the same interval. The implications for stand conversion are clear. If canopy-height female schinus trees are to be killed, it is also important to kill understory seedlings, except where the forest canopy is likely to close very quickly. If this precaution is not taken, the understory schinus seedlings are likely to grow very rapidly, and capture the gap created by the death of the parent tree.

It was anticipated that the death of a mature female schinus tree might have 2 kinds of impacts on the colonization of the understory (and possibly gap capture) by new schinus seedlings. First, the gap creation might affect the ground-level environment in ways that could enhance or reduce schinus germination and establishment. Second, the loss of the overstory female might reduce seed input to the forest floor, and thereby decrease the abundance of understory schinus seedlings. For these reasons schinus seedling densities, germination, and mortality were monitored beneath killed and control trees.

In old schinus forest no. 2 and in the Myrica-schinus woodland, there was less schinus germination beneath killed trees than beneath controls in the first and second fruiting seasons following treatment of the mature females (Fig. 31). In the young schinus forest, schinus germination was about the same in treatment and control plots during the first year, but by the second year it was dramatically reduced beneath treated trees. In old schinus forest no. 1 germination was about the same the first and second years after treatment, but in the second year there was more germination beneath the treated tree than beneath the control. Thus, killing of overstory females was only partially effective in reducing schinus seedling germination in the understory.

After treatment of canopy trees, there were consistently fewer schinus seedlings beneath treated trees than beneath controls, except Jan.-Mar., 1980 in old schinus forest no. 1 (Fig. 32). These reductions in seedling density are especially dramatic when one considers that the pilot study involved only selected individuals in dense schinus stands. Under such conditions dispersal into the gap from surrounding trees might be expected to compensate for the loss of seed input from an overstory parent tree, but that was not the case. The schinus seedlings beneath female trees derive primarily from that female, and death of the parent tree can substantially reduce understory colonization by new schinus seedlings.

The leaf area index (LAI) of the understory vegetation increased on all sites in the first 8 mo following treatment of overstory schinus trees, then decreased during the following year (Table 20). Only part of the increase was caused by growth of previously established schinus seedlings. On 1 site (old schinus forest no. 1) the increase in understory LAI was due primarily to growth of another exotic plant: Ardisia solanacea. In most cases, however, the increased understory LAI was due to growth of native species, but most of these native gap-colonizers

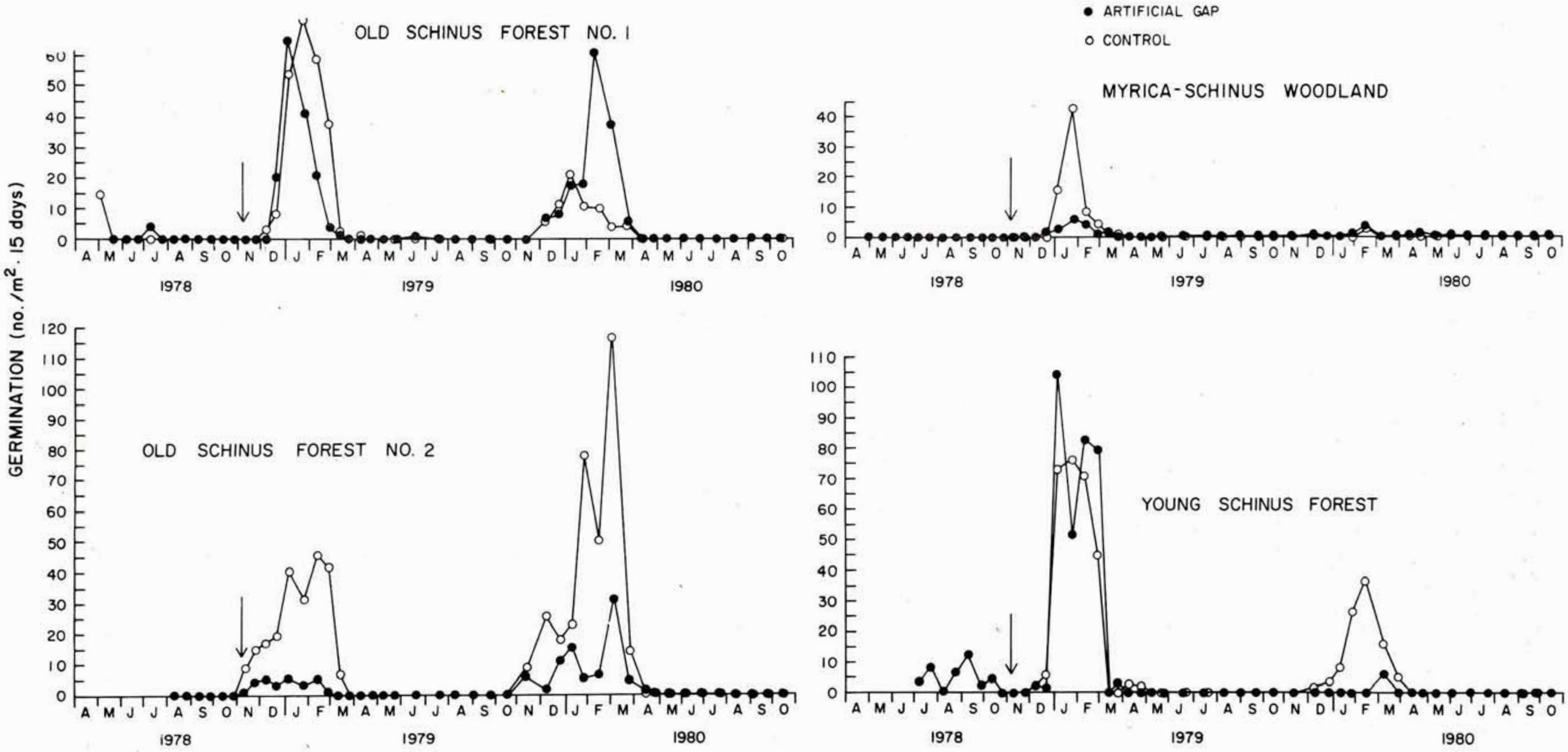


Fig. 31. Germination of schinus seedlings in gaps and beneath schinus-forest canopies on 4 sites. Arrow indicates date of herbicide application to canopy tree.

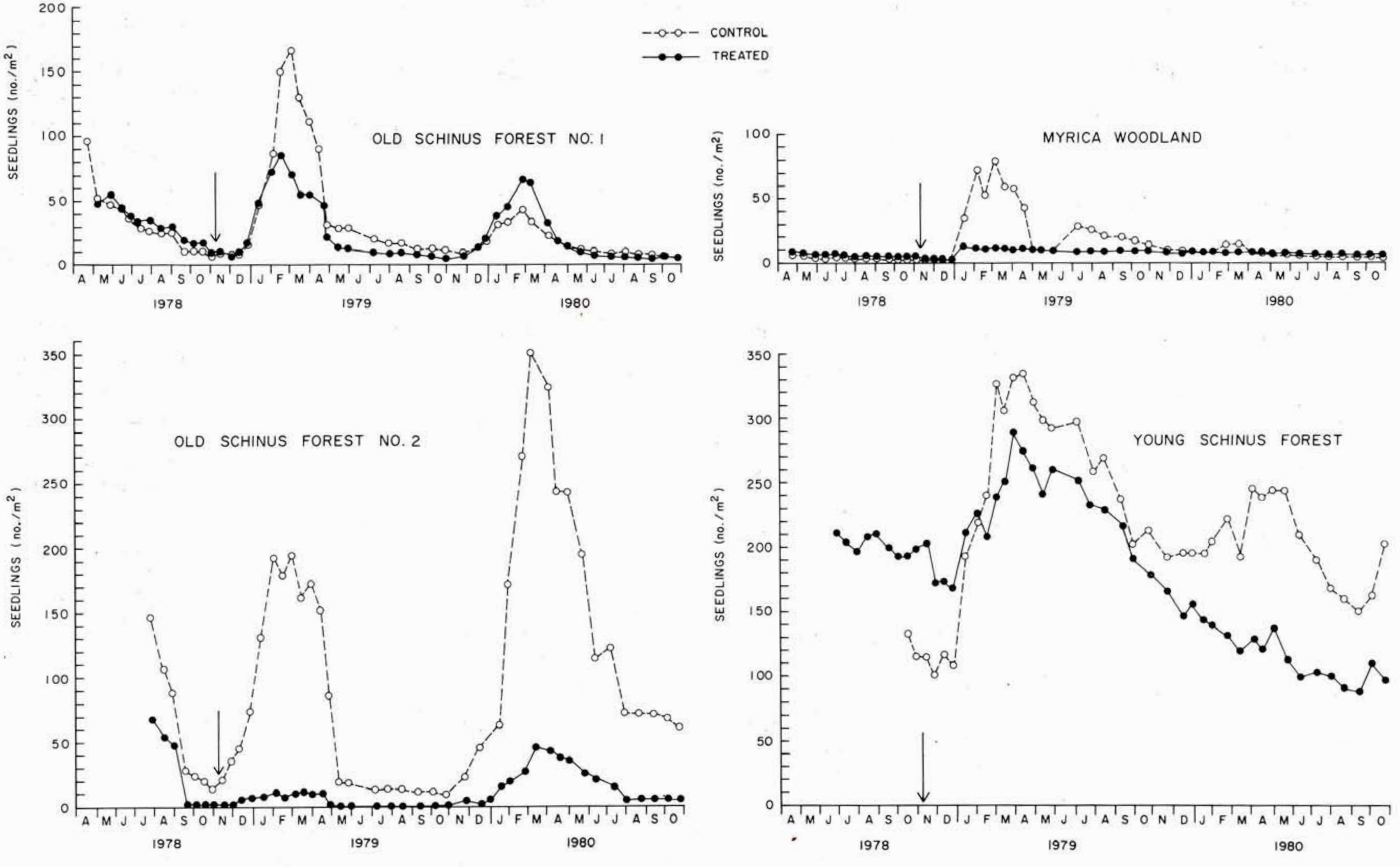


Fig. 32. Schinus seedling density in gaps and beneath schinus-forest canopies on 4 sites. Arrow indicates date of herbicide application to canopy tree.

Table 20. Understory (<0.5 m tall) leaf area index in artificial gaps and in control plots, 8 and 20 mo after herbicide application to canopy female schinus trees. Each value is a mean of 240 sample points (200 for young schinus forest) 8 mo after treatment, and 120 sample points (100 for young schinus forest) 20 mo after treatment.

	Leaf area index					
	Schinus		Other exotics		Total	
Site	After 8 months	After 20 months	After 8 months	After 20 months	After 8 months	After 20 months
Artificial gap						
Old schinus forest no. 1	0	0	0.40	0.38	0.63	0.56
Old schinus forest no. 2	0	0.03	0.01	0	0.54	0.44
Myrica-schinus woodland	0.25	0.22	0	0	0.34	0.26
Young schinus forest	1.42	0.35	0	0	2.17	0.92
Control						
Old schinus forest no. 1	0	0	0.25	0.19	0.53	0.39
Old schinus forest no. 2	0.02	0.02	0	0	0.17	0.16
Myrica-schinus woodland	0.10	0.01	0	0	0.17	0.05
Young schinus forest	0.56	0.30	0	0	1.25	0.90

were herbaceous plants (especially ferns, on wetter sites) and vines. Some woody shrubs and trees did colonize gaps, but these accounted for a small proportion of the total understory LAI.

Larger-scale Study

The effect of killing mature female schinus trees on canopy structure and composition is summarized in 3 series of leaf area index (LAI) profiles, Figs. 33 through 35. Overstory treatment decreased total LAI by 10 weeks after herbicide application, but by 33 weeks after treatment the form and leaf area of the treated canopies were well on the way to complete recovery. The canopy schinus present after treatment were male trees. Their crowns increased in diameter to fill the gaps resulting from the death of large females, and they helped shade the forest floor. Only in the Myrica-schinus woodland, where there were more trees of Myrica cerifera than of schinus, did the importance of schinus decrease in the canopy following treatment. The Myrica responded well to gap creation, and produced much new leaf tissue, especially in the height interval of 6 to 7 m. Treatment of the understory with herbicide was effective in reducing the abundance of schinus seedlings on all sites, and there was little schinus recolonization because the overstory females were killed.

On no site did schinus constitute measurable amounts of understory LAI following understory treatment, even as long as 7.5 mo after herbicide application (Table 21). Furthermore, the attempt to direct herbicides toward schinus and away from native plants was partially successful. Although total LAI of plants other than schinus decreased following understory treatment (presumably due to unavoidable spraying of some native species), it later increased and approached pre-treatment levels (Table 21). This was due, in part, to the flush of understory growth that accompanied opening of the canopy.

The understory vegetation in old schinus forest no. 1 and in the young schinus forest contained nearly 3 times more species than the understory of the Myrica-schinus woodland (Tables 22 through 24). Schinus seedlings were present before and after treatment, both in plots whose understory was sprayed with herbicides and in control (unsprayed) plots. However, the relative abundance of schinus seedlings was reduced by understory treatment. Species applied as part of the propagule package also showed up in the understory vegetation. However, it was impossible to determine whether these plants resulted from seed added by the investigators or from naturally occurring seed, as all species applied are native to the area and quite common. Germination tests of seeds added gave very low germination percentages, indicating that much of the seed added may have been inviable. Furthermore, many of the species may have seeds with a dormancy requirement and the germination of others might be enhanced by acid or mechanical scarification, as described in the section on GERMINATION. Woody plants that were present in the understory following treatment included Persea borbonia, Psychotria spp., Ilex cassine, Myrsine floridana, and Myrica cerifera. One woody exotic species, Ardisia solanacea, was about equally abundant before and after treatment, but the abundance of another, Psidium guajava, was decreased by treatment of the understory.

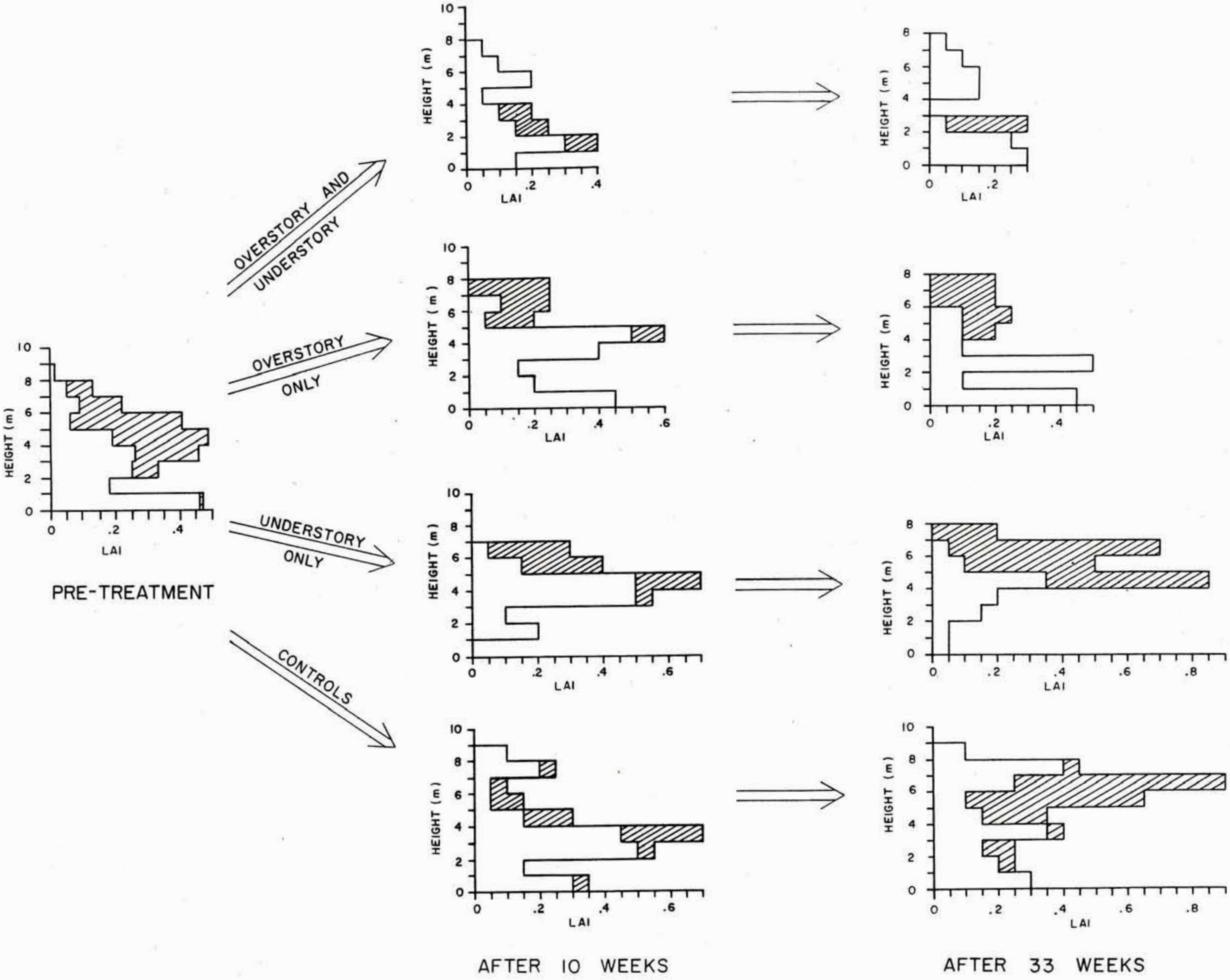


Fig. 33. Changes in vertical distribution of leaf area index (LAI) after 4 herbicide treatments in old schinus forest no. 1. Cross hatching represents schinus foliage. Male schinus trees were not killed as part of overstory treatment. The pre-treatment graph is a mean of 8 trees; others are means of 2 trees.

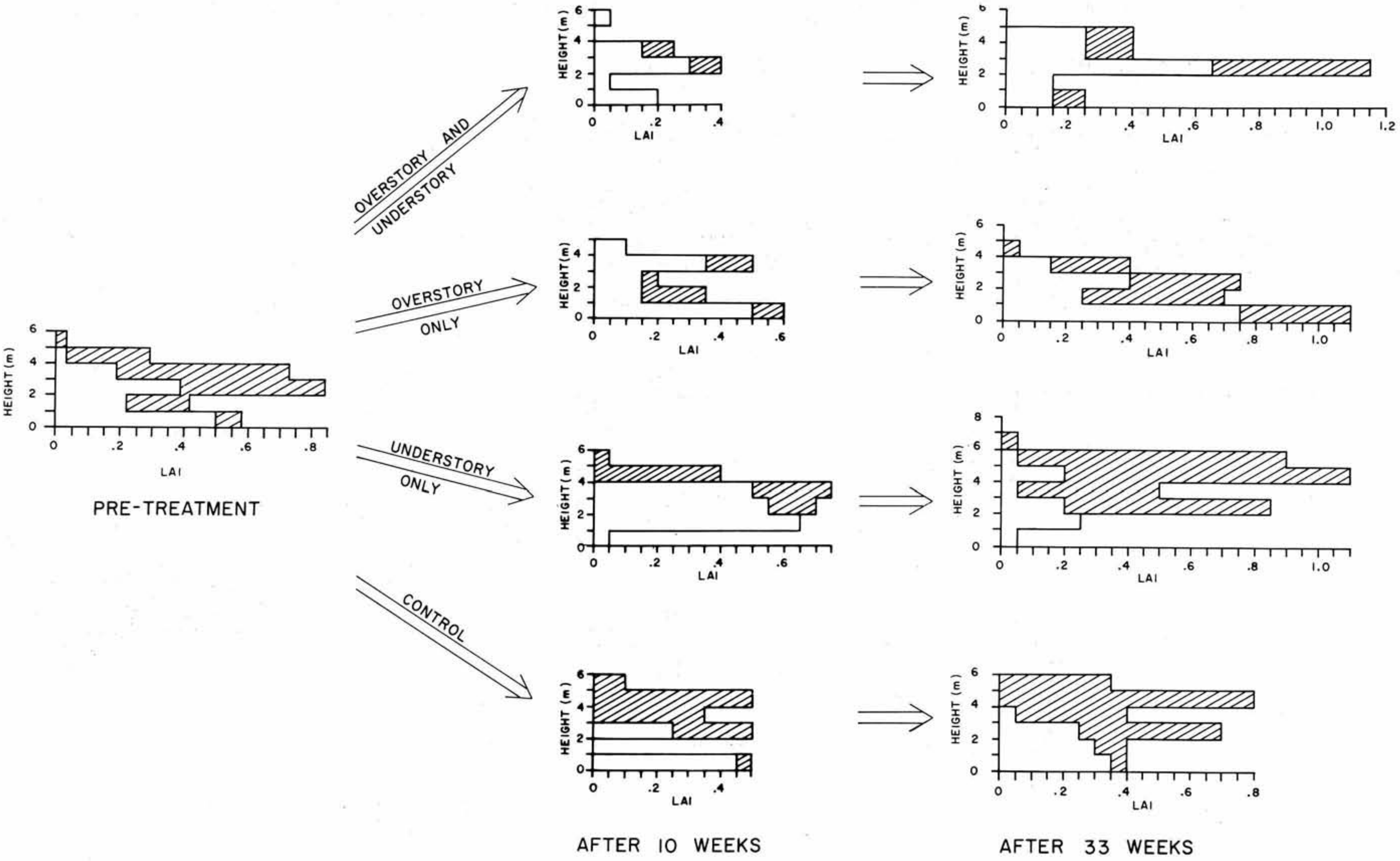


Fig. 34. Changes in vertical distribution of leaf area index (LAI) after 4 herbicide treatments in the young schinus forest. Cross hatching represents schinus foliage. Male schinus trees were not killed as part of overstory treatment. The pre-treatment graph is a mean of 8 trees; others are means of 2 trees.

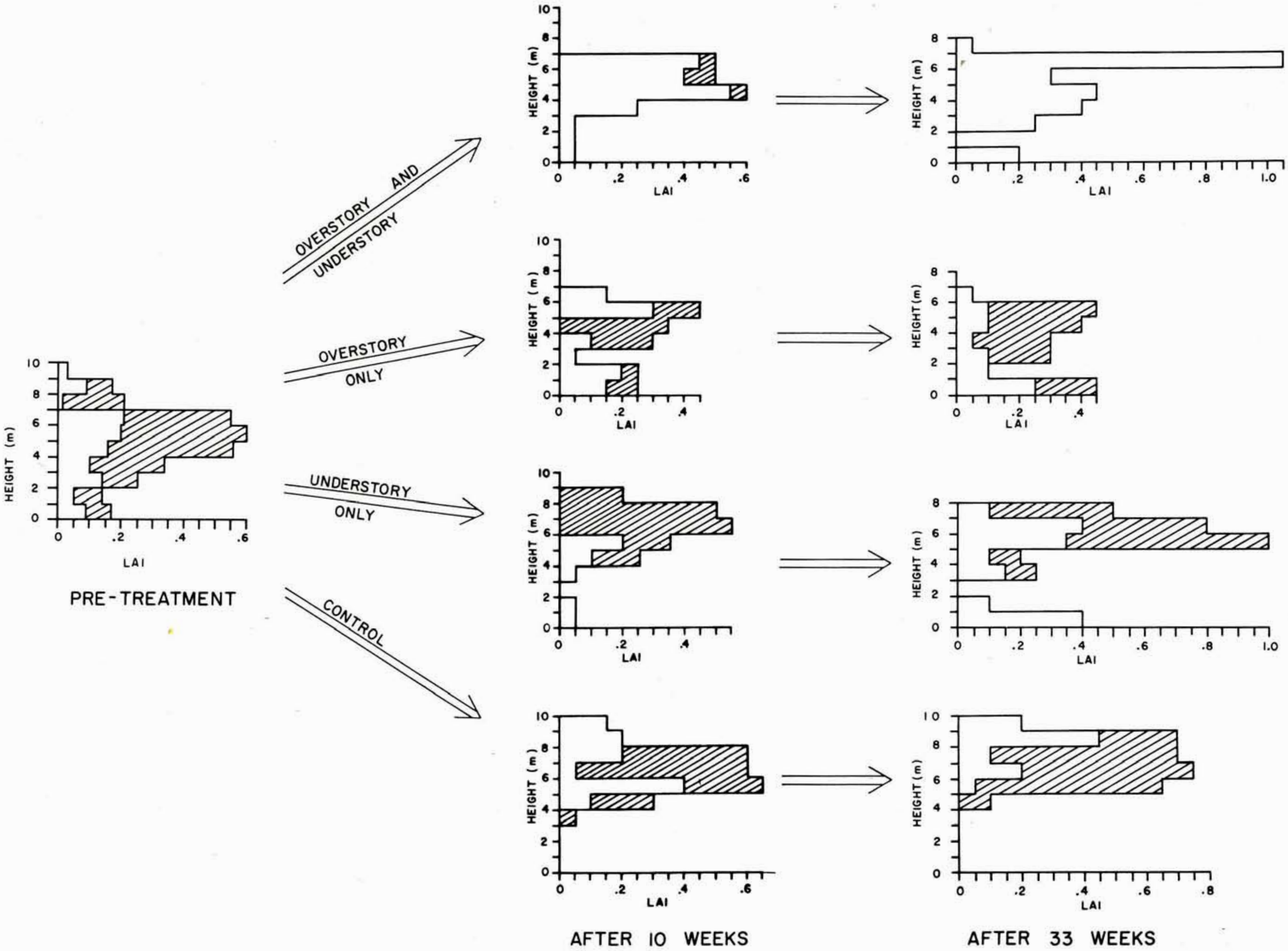


Fig. 35. Changes in vertical distribution of leaf area index (LAI) after 4 herbicide treatments in the Myrica-schinus woodland. Cross hatching represents schinus foliage. Male schinus trees were not killed as part of overstory treatment. The pre-treatment graph is a mean of 8 trees; others are means of 2 trees.

Table 21. Understory (< 0.5 m tall) leaf area index before and after herbicide application in 3 schinus-dominated forests. Each value is a mean of 25 measurements.

			Schinus			Others		
Overstory tree	Understory	Seeds	Before treatment	2.5 months after treatment	7.5 months after treatment	Before treatment	2.5 months after treatment	7.5 months after treatment
			OLD SCHINUS FOREST NO. 1					
Female (killed)	Killed	Added	0.08	0.0	0.0	0.40	0.0	0.12
		Not added	0.0	0.0	0.0	0.76	0.04	0.0
	Not killed	Added	0.20	0.0	0.08	0.52	0.48	0.84
		Not added	0.04	0.08	0.08	0.44	0.28	0.48
Male (not killed)	Killed	Added	0.04	0.0	0.0	0.36	0.0	0.0
		Not added	0.08	0.0	0.0	0.32	0.04	0.0
	Not killed	Added	0.0	0.0	0.0	0.60	0.48	0.36
		Not added	0.0	0.0	0.0	0.20	0.20	0.20
			YOUNG SCHINUS FOREST					
Female (killed)	Killed	Added	0.12	0.0	0.0	0.72	0.0	0.0
		Not added	0.12	0.0	0.0	0.76	0.0	0.04
	Not killed	Added	0.12	0.28	0.28	0.72	0.04	0.44
		Not added	0.04	0.04	0.0	0.56	0.52	1.32
Male (not killed)	Killed	Added	0.0	0.0	0.0	0.80	0.0	0.0
		Not added	0.04	0.0	0.0	0.68	0.08	0.24
	Not killed	Added	0.12	0.0	0.04	0.40	0.68	0.80
		Not added	0.0	0.0	0.0	0.60	0.72	0.96

Table 21. Continued.

Overstory tree	Understory	Seeds	Schinus Before treatment	 2.5 months after treatment	 7.5 months after treatment	Others Before treatment	 2.5 months after treatment	 7.5 months after treatment
			MYRICA-SCHINUS WOODLAND					
Female (killed)	Killed	Added	0.0	0.0	0.0	0.0	0.0	0.0
		Not added	0.04	0.0	0.0	0.04	0.04	0.04
	Not killed	Added	0.04	0.0	0.0	0.12	0.20	0.44
		Not added	0.08	0.16	0.16	0.04	0.04	0.12
Male (not killed)	Killed	Added	0.0	0.0	0.0	0.0	0.0	0.0
		Not added	0.08	0.0	0.0	0.08	0.0	0.04
	Not killed	Added	0.0	0.0	0.0	0.0	0.0	0.0
		Not added	0.0	0.08	0.04	0.0	0.0	0.0

Table 22. Understory (<1 m tall) species composition and abundance before and after herbicide application, old schinus forest no. 1. Values in parentheses are seedlings with cotyledons. Asterisk indicates species included in propagule package. Values are means of 4, 2.5 m^2 plots.

	Abundance (no./m^2)			
	Understory treated		Understory not treated	
Species	3 mo before treatment	2 mo after treatment	3 mo before treatment	2 mo after treatment
1. *Schinus terebinthifolius*	4.3 (28.4)	0.1	8.0 (11.9)	19.5 (17.3)
2. **Baccharis* spp.	5.9 (10.3)		5.3 (29.0)	10.2
3. **Persea borbonia*	5.2	0.6	7.2	16.3
4. **Myrsine floridana*	3.7	1.1 (0.5)	5.8	6.7
5. *Ampelopsis arborea*	1.6	1.8	2.8	9.1
6. *Parthenocissus quinquefolia*	4.3	0.5	0.9	2.4
7. *Psidium guajava*	3.6		4.3	
8. *Psychotria sulzneri* (or *P. nervosa*)	4.2		2.7	
9. *Ardisia solanacea*	1.4	1.7	1.8	1.5
10. *Panicum joorii*	2.8		2.6	
11. **Psychotria ligustrifolia*				5.1
12. *Thelypteris kunthii*	2.8		0.9	1.0
13. **Ilex cassine*	0.3	0.2	1.1	2.5
14. Unknown # 40			(3.1)	
15. *Toxicodendron radicans*		1.9		0.4
16. *Salix caroliniana*			1.7	0.2
17. *Vitis rotundifolia*	0.2			1.4
18. *Rhus radicans*	1.1		0.4	
19. Unknown grass #53				1.0
20. *Boehmeria cylindrica*	0.5		0.2	0.2
21. *Hyptis alata*			0.4	0.3
22. *Cissus sissyoides*	0.3		0.1	0.1
23. *Vigna luteola*	0.4		0.1	
24. *Vicia acutifolia*				0.4

Table 22. Continued.

Species	Abundance (no./m^2) Understory treated: 3 mo before treatment	Understory treated: 2 mo after treatment	Understory not treated: 3 mo before treatment	Understory not treated: 2 mo after treatment
25. Unknown grass # 43	0.4			
26. *Quercus virginiana*				0.4
27. *Galium obtusum*			0.2	0.1
28. *Mikania scandens*	0.2			
29. *Zeuxine strateumatica*	0.2			
30. *Verbena scabra*			0.2	
31. Unknown # 41			(0.1)	
32. *Hypericum* sp.	0.1			
33. Unknown # 49	0.1			
34. *Eulophia alta* (?)			0.1	
35. *Erechtites hieracifolia*				0.1

Table 23. Understory (<1 m tall) species composition and abundance before and after herbicide application, young schinus forest. Values in parentheses are seedlings with cotyledons. Asterisk indicates species included in propagule package. Values are means of 4, 2.5 m^2 plots.

	Abundance (no./m^2)			
	Understory treated		Understory not treated	
Species	3 mo before treatment	2 mo after treatment	3 mo before treatment	2 mo after treatment
1. *Schinus terebinthifolius*	30.2 (8.7)	0.6 (0.2)	19.5 (7.7)	23.3 (11.1)
2. **Baccharis* spp.	2.4 (61.2)		2.1 (48.3)	9.5 (5.7)
3. *Galium obtusum*	5.4		15.0	3.3
4. *Thelypteris kunthii*	7.0	0.3	4.2	4.4
5. *Hydrocotle umbellata*			11.6	2.3
6. *Boehmeria cylindrica*	5.1		4.8	2.0
7. *Borreria laevis*	2.6	0.1	3.7	3.1 (0.3)
8. *Andropogon glomeratus*	0.2		2.5	3.0
9. *Eupatorium coelestinum*	1.3		1.4	0.5
10. **Myrica cerifera*	1.0		0.3	0.9
11. *Mikania scandens*	0.5		0.6	0.4
12. *Vigna luteola*	0.3		0.2	0.9
13. Unknown #68				1.3
14. *Sida acuta*	0.2		0.1	0.9
15. *Parthenocissus quinquefolia*			0.3	0.8
16. *Eustachys glauca*			1.0	
17. *Lysiloma bahamense*	1.0			
18. *Ludwigia microcarpa*			0.5	0.5
19. *Melothria pendula*	0.9			
20. *Solidago stricta*			0.3	0.5
21. *Vitis rotundifolia*	0.1	0.4		0.2
22. *Erechtites hieracifolia*				0.6
23. *Verbena scabra*	0.2		0.4	

Table 23. Continued.

	Abundance (no./m^2)			
	Understory treated		Understory not treated	
Species	3 mo before treatment	2 mo after treatment	3 mo before treatment	2 mo after treatment
24. Unknown grass #70				0.5
25. **Ludwigia peruviana*	0.2		0.3	
26. *Mecardonia vandellioides*			0.1	0.3
27. *Vicia acutifolia*	0.3			
28. **Persea borbonia*			0.1	0.1
29. Unknown #69 (sedge?)				0.1
30. *Commelina diffusa*	0.1			
31. *Cynanchum scoparium*	0.1			
32. *Sporobolus* sp.			0.1	
33. *Cynoctonum mitreola*			0.1	
34. **Ludwigia octovalvis* (?)				0.1

Table 24. Understory (< 1 m tall) species composition and abundance before and after herbicide application, Myrica-schinus woodland. Values in parentheses are seedlings with cotyledons. Asterisk indicates species included in propagule package. Values are means of 4, 2.5 m^2 plots.

	Abundance (no./m^2)			
	Understory treated		Understory not treated	
Species	3 mo before treatment	2 mo after treatment	3 mo before treatment	2 mo after treatment
1. Schinus terebinthifolius	2.0 (1.7)	0.2	2.1 (1.2)	2.2 (0.2)
2. Morinda royoc	1.0	0.6	1.9	1.2
3. *Myrica cerifera	0.4		1.4	1.1
4. *Tetrazygia bicolor	0.1		0.4	0.2
5. *Myrsine floridana	0.1	0.2	0.2	
6. Unknown #72	0.5			
7. *Baccharis spp.	(0.2)		(0.2)	
8. Chiococca parvifolia	0.3			
9. Parthenocissus quinquefolia			0.2	
10. Oxalis stricta			0.1	0.1
11. Vitis rotundifolia				0.1
12. Unknown #73			0.1	
13. Unknown #74 (monocot)			0.1	

Understory treatment with herbicides did not significantly reduce the abundance of trees and shrubs > 1 m tall beneath canopy-height female schinus trees (Tables 25 through 27). This is important because it is these plants, more than the herbs and vines of the lower understory, that are likely to capture the gap created by the death of canopy trees. Schinus was an important understory shrub on all 3 sites, and can be expected to be important in gap capture. Undoubtedly many of these schinus bushes will be females (anticipated 50%), so stand conversion will require at least 2 treatments of female trees, and possibly more. On former glade sites Myrsine floridana and Baccharis spp. are important shrubs, while Myrica cerifera is the most abundant shrub on the former pine site. The fact that Myrica is allelopathic to schinus (Dunevitz and Ewel 1980) may facilitate the conversion of schinus-dominated forests on former pine sites to woodlands dominated by Myrica and other species characteristic of pinelands, such as Guettarda scabra and Tetrazygia bicolor. However, no pines were observed in study plots on former pineland, even though the nearest pine seed source was < 200 m away.

Matricide seems to offer one promising method of schinus stand conversion. It is not a dramatic technique. Nor is it extremely disruptive of the community being converted. It has been shown to reduce the reproductive potential of schinus on the local level, and it seems obvious that it will also reduce the potential for schinus invasion into surrounding ecosystems. However, it must be done carefully to assure that overstory females are killed and that understory schinus do not capture the gaps created by the death of overstory trees. Furthermore, more than 1 treatment will be required to convert a forest, and it is not a technique designed to eliminate schinus, but only to gradually reduce its dominance. The data indicate that canopy-height male schinus trees should not be killed, as their shade inhibits growth of understory schinus seedlings. If the technique is successful, these canopy-height male trees will eventually be replaced through natural attrition by native species with similar site requirements.

SEED MOVEMENTS AND SOIL SEED BANKS

In addition to research that emphasized schinus, studies were also conducted to determine the amounts and composition of seed flows among, and seed storages within, both mature and successional ecosystems in the study area. Studies of seed fluxes and soil seed storage were thought to be important as part of the present study for 2 reasons. First, they tell us what species are potentially emigrating out of weed- and exotic-laden successional ecosystems into surrounding mature communities. Second, vegetation change toward a more mature community can occur only if seeds get from the mature ecosystems into the successional vegetation. Even if the environmental conditions on released farmland are amenable to recolonization by the original flora, this recolonization cannot occur unless the necessary seeds reach the sites.

Seed dispersal is the main means by which non-mobile plants get from one place to another. Some dispersed seeds germinate, some die and decay, some are consumed by animals and microbes, and some accumulate in the soil as a living seed bank. Seeds of some species are very short-lived

Table 25. Shrubs and trees (> 1 m tall) beneath schinus trees, before and after understory herbicide application, old schinus forest no. 1. Values are means of 4, 2.5 m^2 plots.

	Abundance (no./m^2)			
	Understory treated		Understory not treated	
Species	3 mo before treatment	2 mo after treatment	3 mo before treatment	2 mo after treatment
1. *Schinus terebinthifolius*	0.1	0.0	0.0	0.1
2. *Myrsine floridana*	1.5	1.2	3.2	2.9
3. *Baccharis* spp.	0.3	0.0	2.0	0.6
4. *Ilex cassine*	0.0	0.0	3.0	0.0
5. *Cissus sissyoides*	0.3	0.0	0.0	0.0
6. *Ardisia solanacea*	0.1	0.1	0.0	0.1
7. *Persea borbonia*	0.0	0.0	0.1	0.1
8. *Myrica cerifera*	0.0	0.0	0.0	0.2
9. *Ampelopsis arborea*	0.0	0.0	0.0	0.2
10. *Toxicodendron radicans*	0.0	0.1	0.0	0.0

Table 26. Shrubs and trees (>1 m tall) beneath schinus trees, before and after understory herbicide application, young schinus forest. Values are means of 4, 2.5 m^2 plots.

	Abundance (no./m^2)			
	Understory treated		Understory not treated	
Species	3 mo before treatment	2 mo after treatment	3 mo before treatment	2 mo after treatment
1. *Schinus terebinthifolius*	0.3	0.4	1.0	1.0
2. *Baccharis* spp.	0.3	0.2	0.5	0.5
3. *Vitis rotundifolia*	0.1	0.3	0.1	0.0
4. *Myrica cerifera*	0.0	0.0	0.1	0.2
5. *Sarcostemma clausa*	0.0	0.1	0.0	0.0
6. *Vigna luteola*	0.0	0.0	0.0	0.1
7. *Mikania scandens*	0.0	0.0	0.0	0.1
8. *Persea borbonia*	0.0	0.1	0.0	0.0

Table 27. Shrubs and trees (>1 m tall) beneath schinus trees, before and after understory herbicide application, *Myrica*-schinus woodland. Values are means of 4, 2.5 m^2 plots.

	Abundance (no./m^2)			
	Understory treated		Understory not treated	
Species	3 mo before treatment	2 mo after treatment	3 mo before treatment	2 mo after treatment
1. *Myrsine floridana*	0.1	0.0	0.1	0.0
2. *Morinda royoc*	0.0	0.0	0.1	0.0
3. *Tetrazygia bicolor*	0.0	0.0	0.1	0.1
4. *Schinus terebinthifolius*	0.1	0.1	0.0	0.0
5. *Myrica cerifera*	0.3	0.2	0.0	0.1

once they reach the soil, while others can survive for years. The movement and soil storage of seeds are major factors in determining the course of succession.

Methods

Seed Trapping

The seed trapping technique consisted of placing 10 traps in each ecosystem (8 on some dates in the 1973 succession). To assure capture of immigrating seeds, the traps were concentrated near community boundaries in all cases except the control treatments of the 8 Hilsenbeck succession plots, where 1 trap was placed in each plot. On all other sites the traps were located inward from the ecosystem boundary at the following distances: 1, 2, 4, 8, 16, 32, 64, 154, and 199 m.

Each seed trap was a 0.168 m^2 galvanized metal greenhouse tray containing vermiculite covered with 3-7 cm of soil. The soil was rock-plowed marl gathered from the study area, and was sterilized at 100° C for 4 h before use. The traps were covered with dense-weave nylon cloth during transport to avoid contamination by other seeds. Shallow depressions were dug at each seed trap location so that the upper surface of the trap was only slightly higher than the surrounding soil surface. During the wet season some traps were flooded, as was the soil around them.

After a period in the field (usually 30 days, but see Fig. 36), the seed traps were covered and transported to a seed-free shadehouse (60% shade cloth), then uncovered. At this time 3 control traps (prepared at the same time, but never placed in the field) were also uncovered in the shadehouse to check for possible seed contamination, either because seeds penetrated the shadehouse or because the sterilization procedure did not kill all seeds in the soil. All flats were kept well watered (rainwater or study-area well water), and seedlings that germinated were counted and identified. Unidentifiable seedlings were transplanted into pots and grown until they reached a stage when identification was possible.

This seed trapping technique measures only the input of viable seeds that germinate while the trap is in the field or during the interval (usually 4 mo, but range of 1 to 5) while the trap is in the shadehouse. It does not measure input of nonviable seed nor seeds whose germination is long delayed. However, a previous study (Ewel and Conde 1979) in the same area indicated that most seeds and species germinated within 30 days.

Soil Seed Storage

The amount and species composition of the soil seed bank was studied on the same sites where seeds were trapped, plus several others (Fig. 36). Samples were taken at randomly selected locations. Usually 4 (sometimes 5) samples were taken per site at each sampling time. Each sample was obtained by driving a sharpened pipe, 12.9 cm in diameter, into the soil and removing the soil within to a depth of 2-6 cm. The soil from each 130.7 cm^2 sample was then spread over vermiculite in a

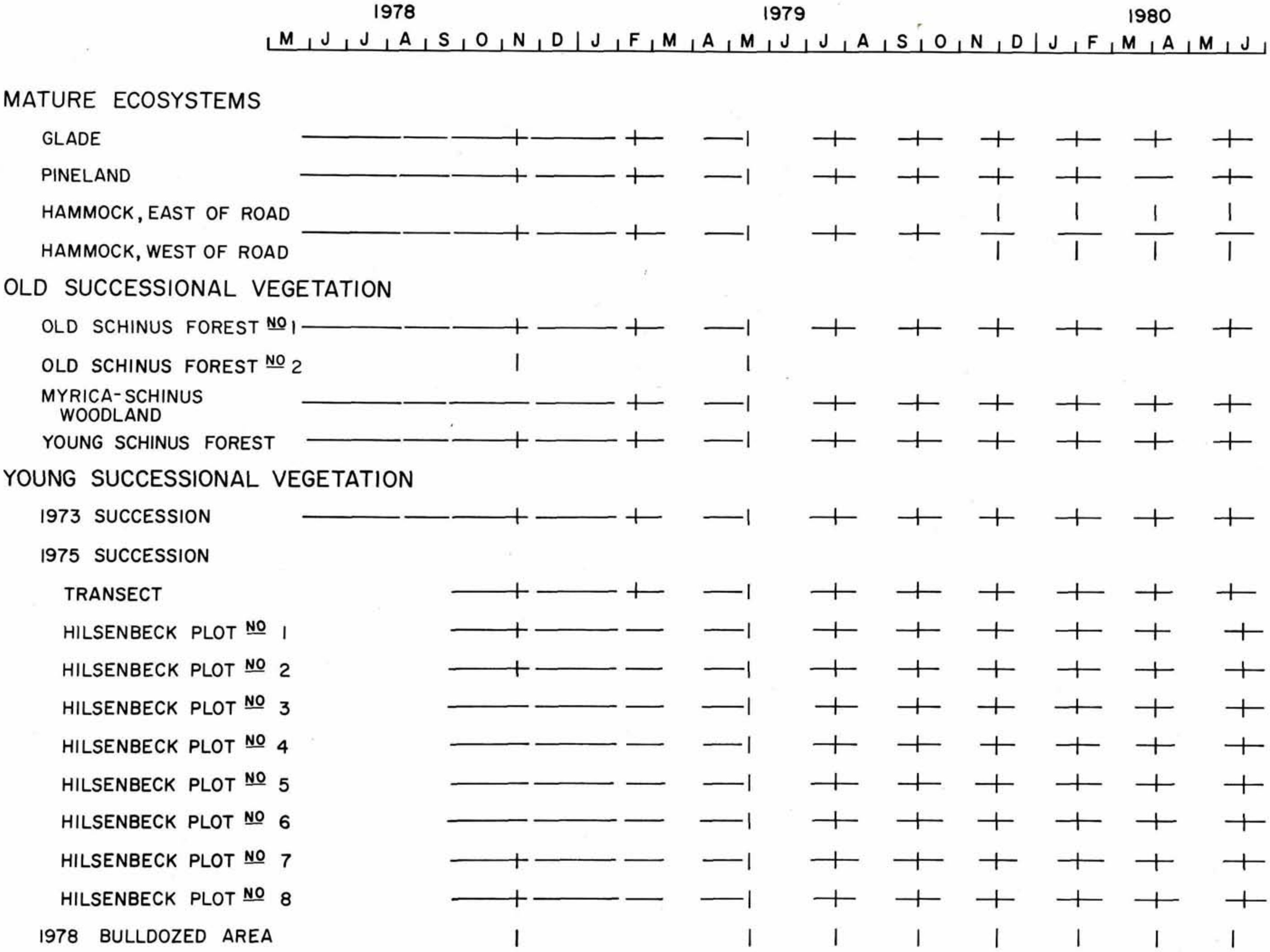


Fig. 36. Dates of seed trapping and soil-seed-bank sampling. Horizontal bars are dates when seed traps were in the field. Vertical bars indicate field sampling dates for soil-seed-bank measurement.

13.2 cm diameter (= 136.8 cm^2) pot and placed in the seed-free shadehouse. The samples were watered regularly, and seeds that germinated were identified and counted. Samples were retained in the shadehouse for an average of 4 mo.

Impact of Pineland Burn

The pineland study site was subjected to a prescribed burn on 29 Nov. 1979, while a set of seed traps was in the field. The traps had been there since 15 Nov. and were removed 12 Dec. To evaluate the impact of the burn on seed fluxes, a set of 10 traps was returned to the pineland site on 13 Dec. and removed 16 Jan. Also, on 7 Dec., 20 soil samples, of 130.7 cm^2 each, were taken to assess the impact of the fire on the soil seed bank. The results obtained with those samples were compared with those from the 4 samples that had been harvested the morning before the burn.

Results

Seed Trapping

There was considerable variability in the numbers of germinable seeds trapped and in the number of species trapped, both among sites and among seasons at the same site (Fig. 37). There were, however, consistent trends among groups of ecosystems. The mature communities (glade, pineland, and hammock) tended to have lower amounts of seed rain (usually < 40 seeds $\cdot\ m^{-2} \cdot day^{-1}$), and their traps seldom captured > 20 species during any given trapping interval. The intermediate-aged forests (old schinus forest, *Myrica*-schinus woodland, and young schinus forest) had consistently higher seed rain than the mature communities. Their seed rains contained more species, as well: frequently > 20 species per trapping interval. The greatest amounts of seeds, as well as the most diverse seed floras, were trapped in the 2 young successional vegetations. Seed rains there were regularly > 100 viable seeds per m^2 per day. The Nov.-Dec., 1979 trapping interval resulted in the capture of about 300 and 500 seeds per m^2 per day in the 1975 and 1973 successions, respectively.

The seed rain data (Fig. 37) nicely confirm the generalization that species characteristic of young successional vegetation make great investments in reproduction. Vast numbers of propagules, of many species, were produced throughout the year. As the successional ecosystems in the study area age they can be expected to be less prodigious producers of seeds, and therefore less likely to pose as strong a threat of mature-community invasion as they do now. However, successional species are notoriously responsive, and their populations can be expected to burgeon following ecosystem disturbance.

The flora of the study area is like that of many moist tropical and subtropical regions in that it produces seeds during all seasons. The one time that there is a predictable dip in the seed rain at most sites is mid-winter. Site conditions may be amenable to colonization at that time, but the decrease in seed output may simply reflect the fact that much of South Florida's flora is of north-temperate origin, and many of

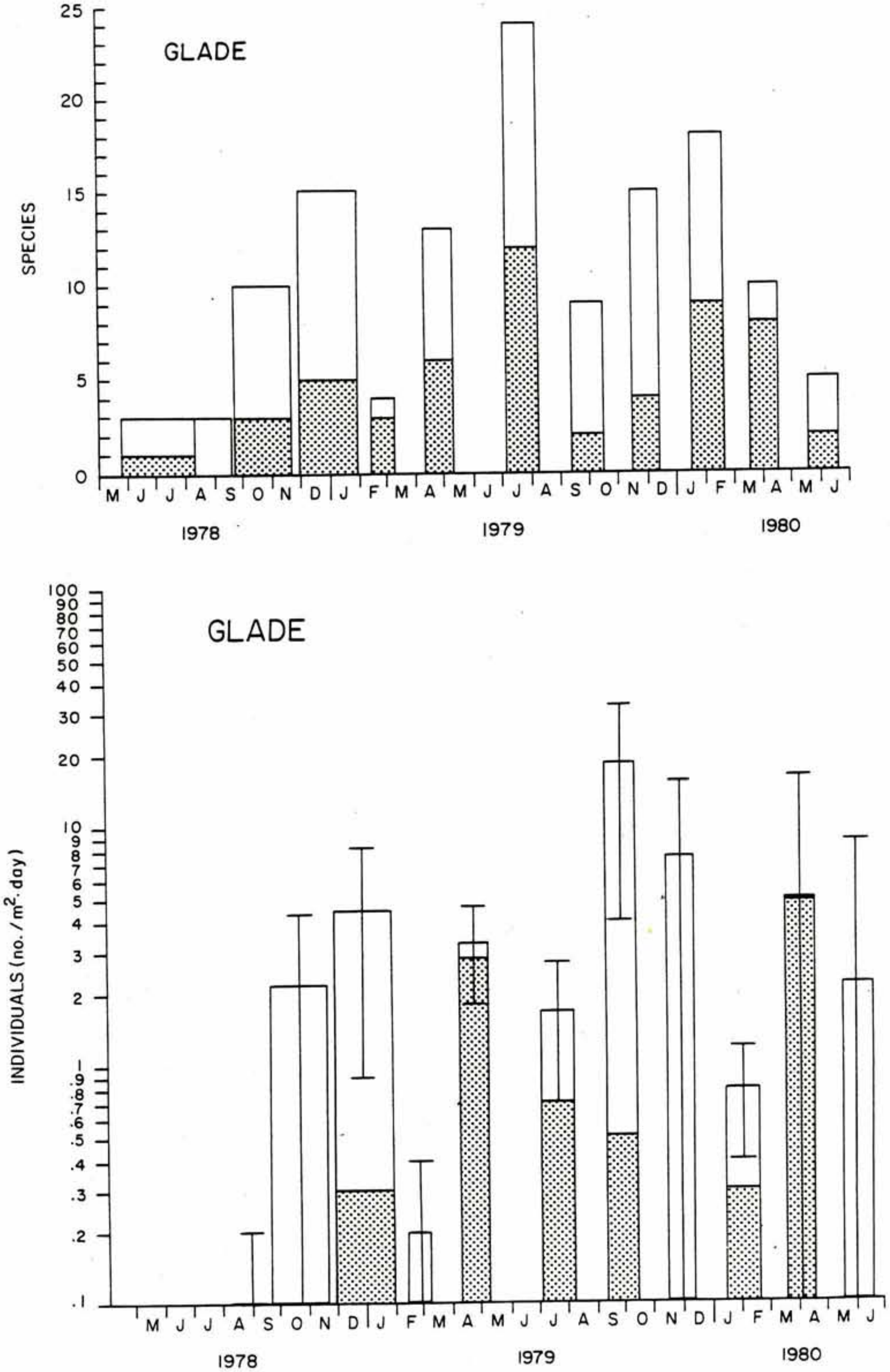
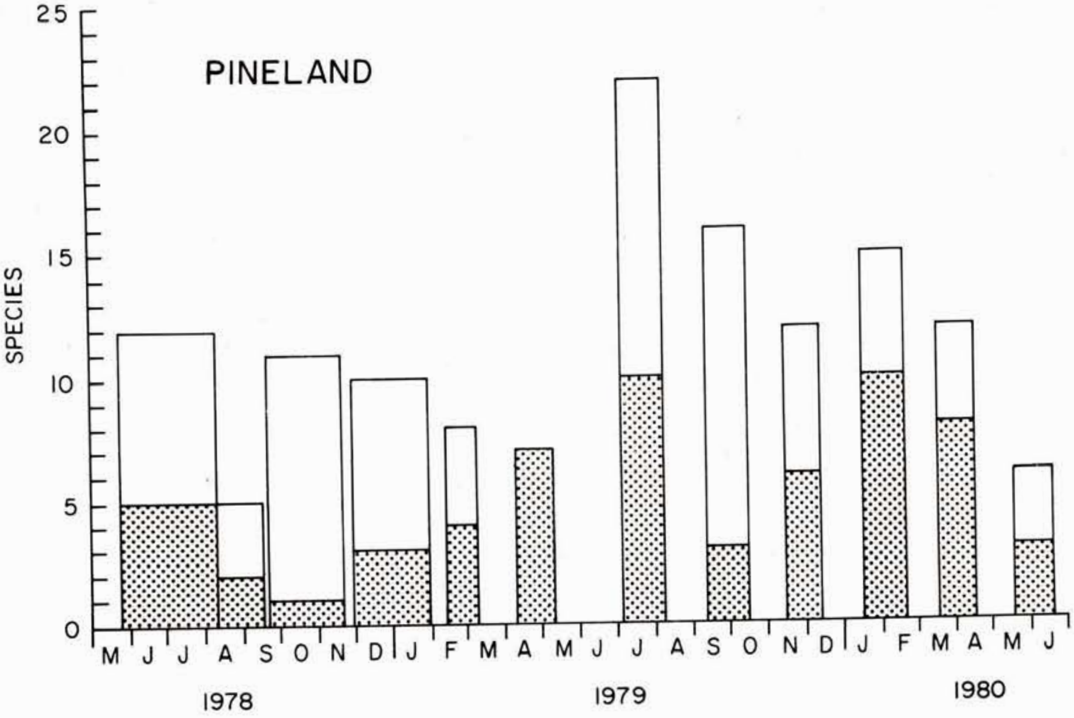


Fig. 37. Number of species and number of germinable seeds trapped in 8 sites. Bar width represents time traps were in field. Shading indicates weedy species; open bars are non-weedy species. Vertical lines are ± 1 standard deviation. Most bars on the 1975 succession graph are divided vertically. The left half are data from the 1975 succession transect, and the right half are data from the 1975 succession Hilsenbeck plots. Undivided bars include data from the transect only.



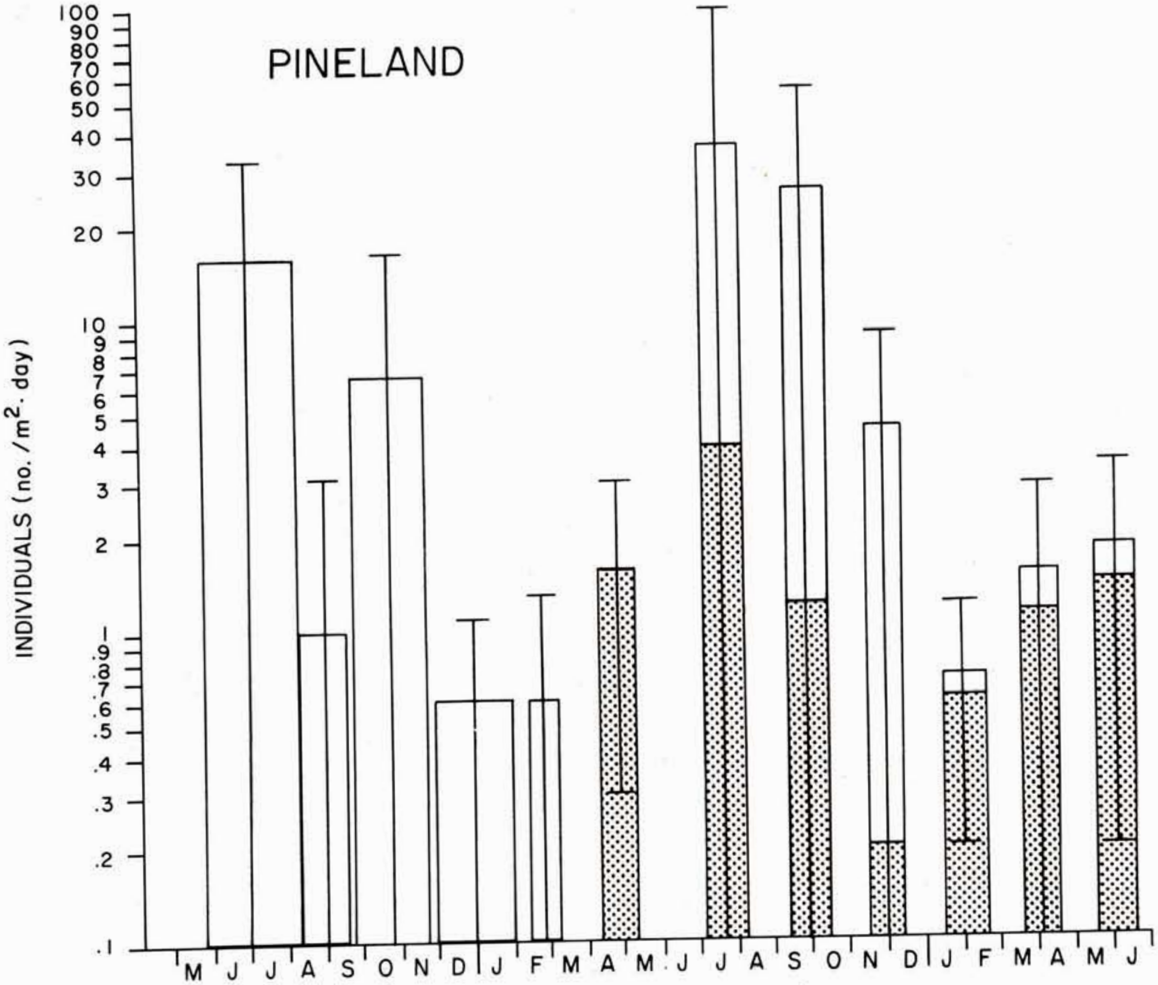
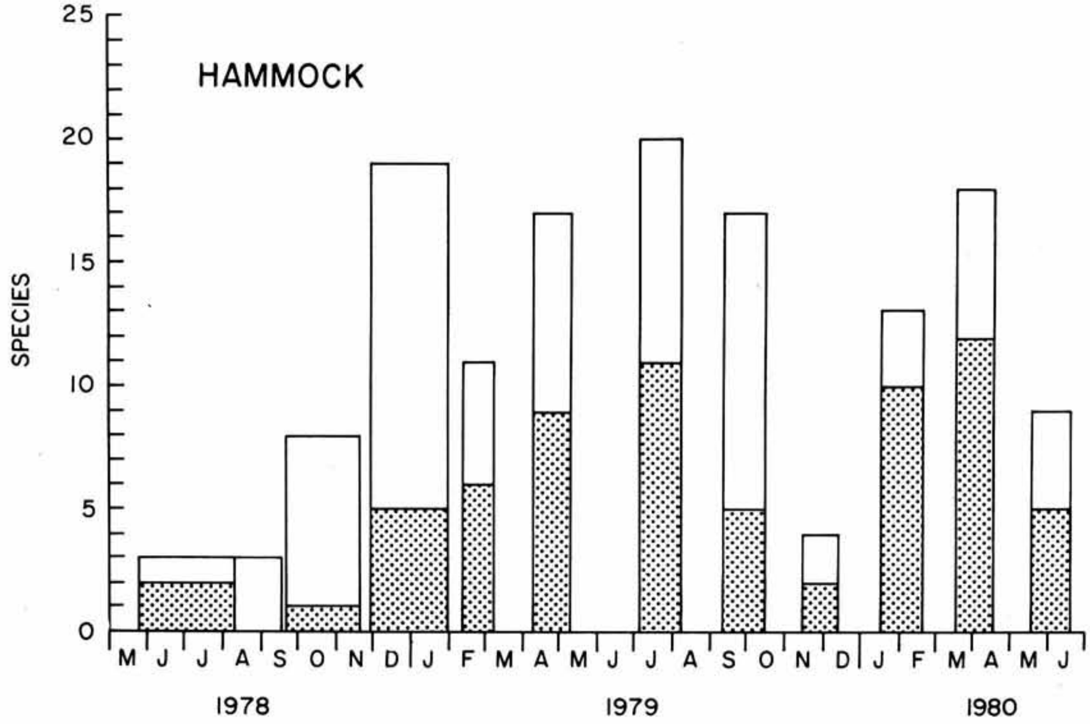


Fig. 37. Continued.



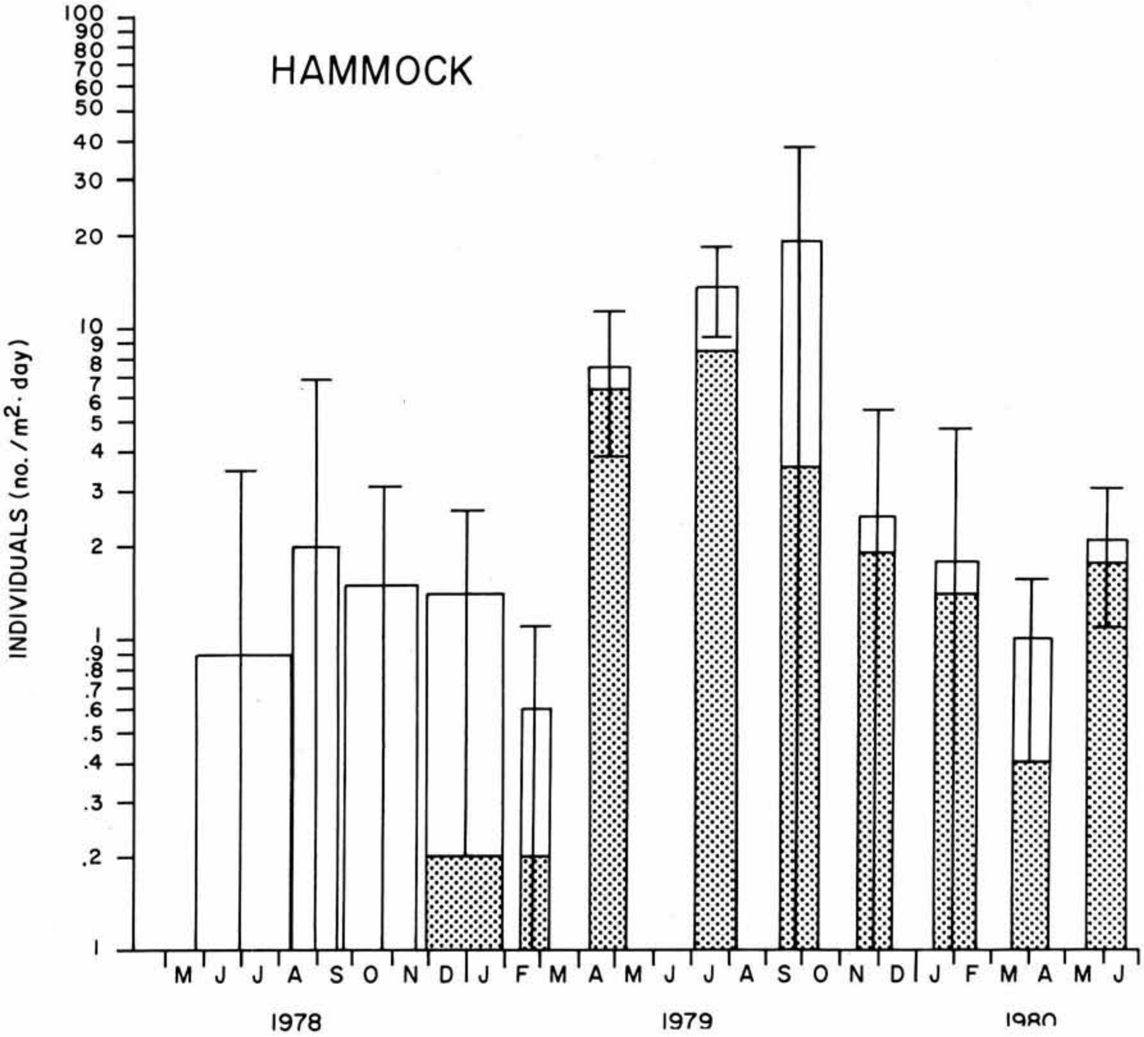
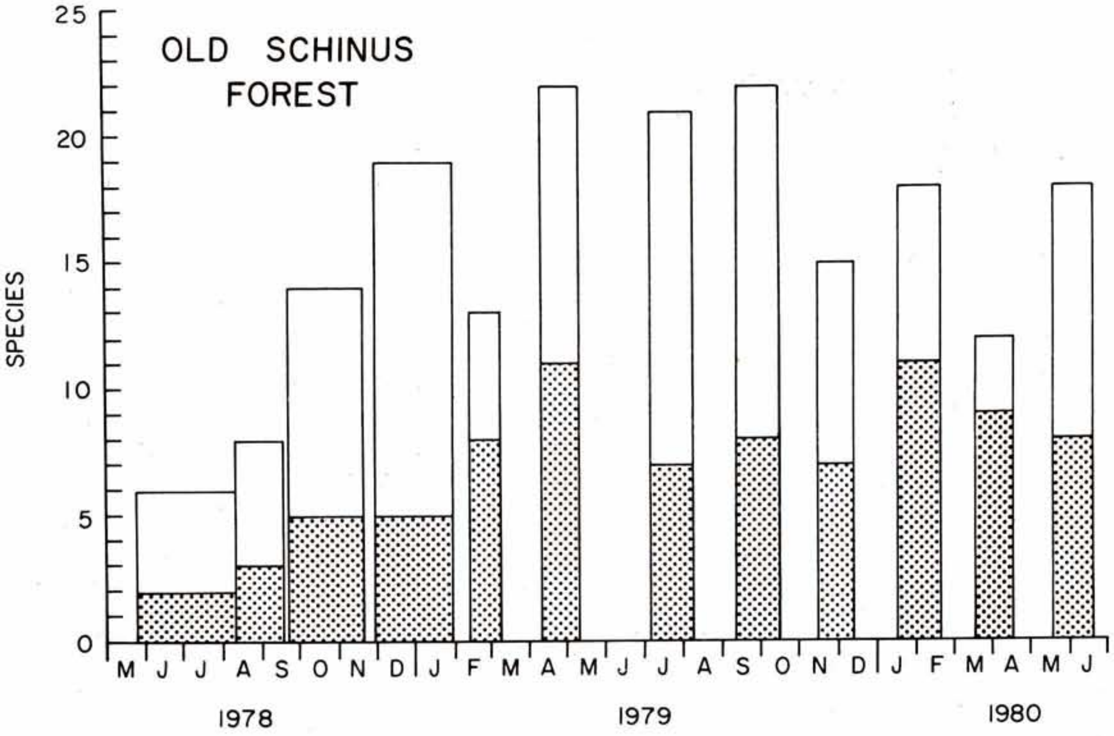


Fig. 37. Continued.



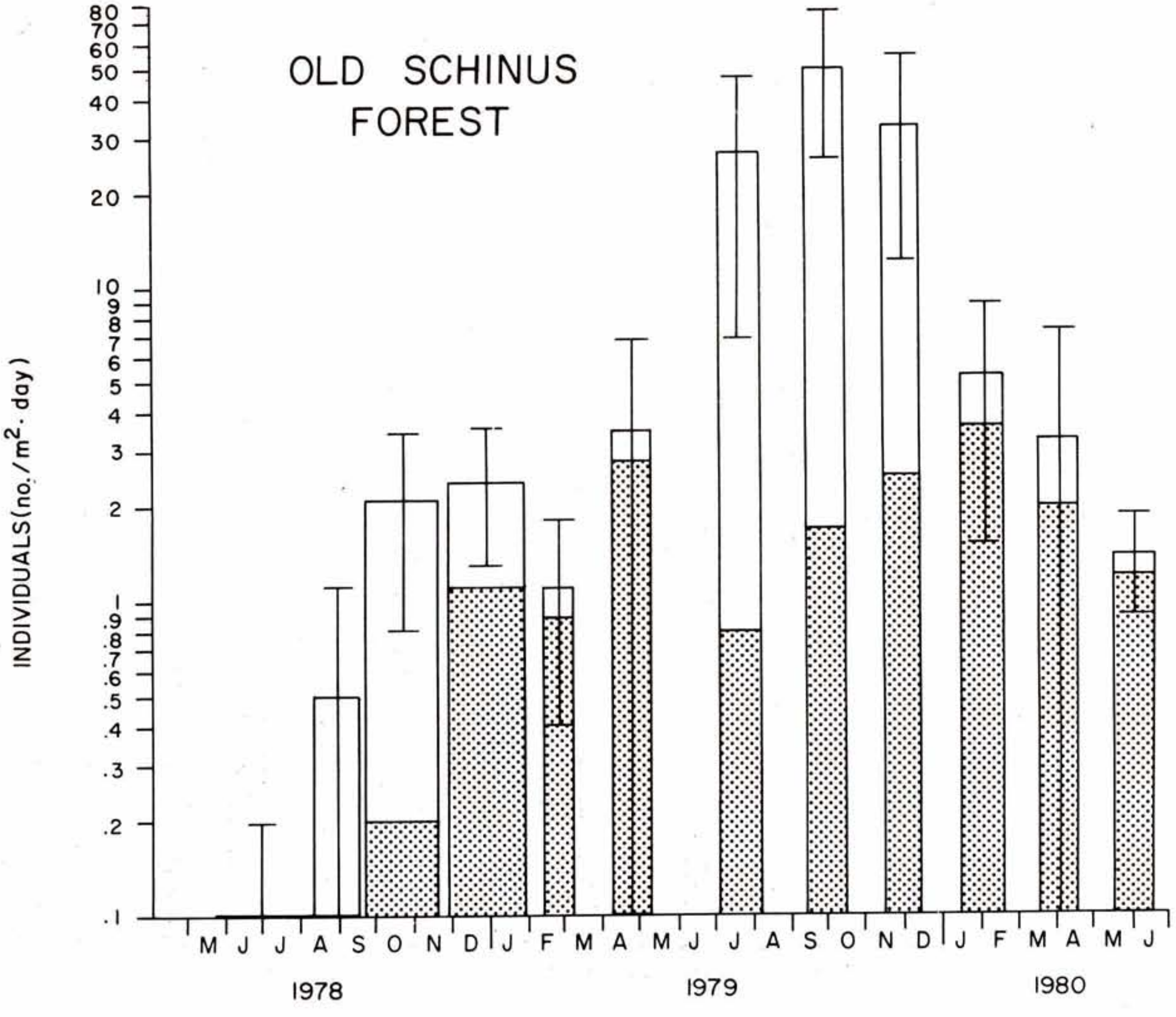


Fig. 37. Continued.

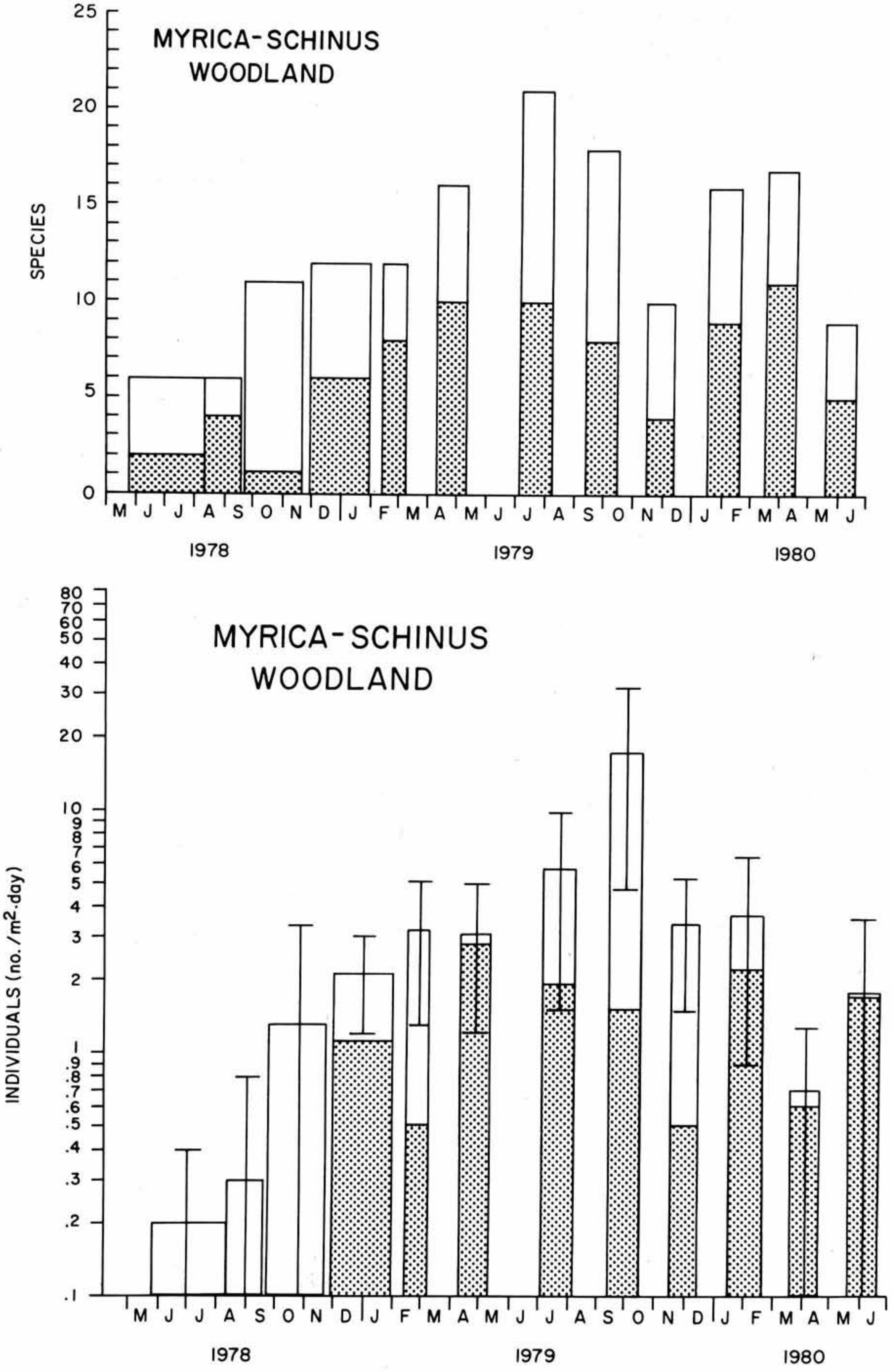
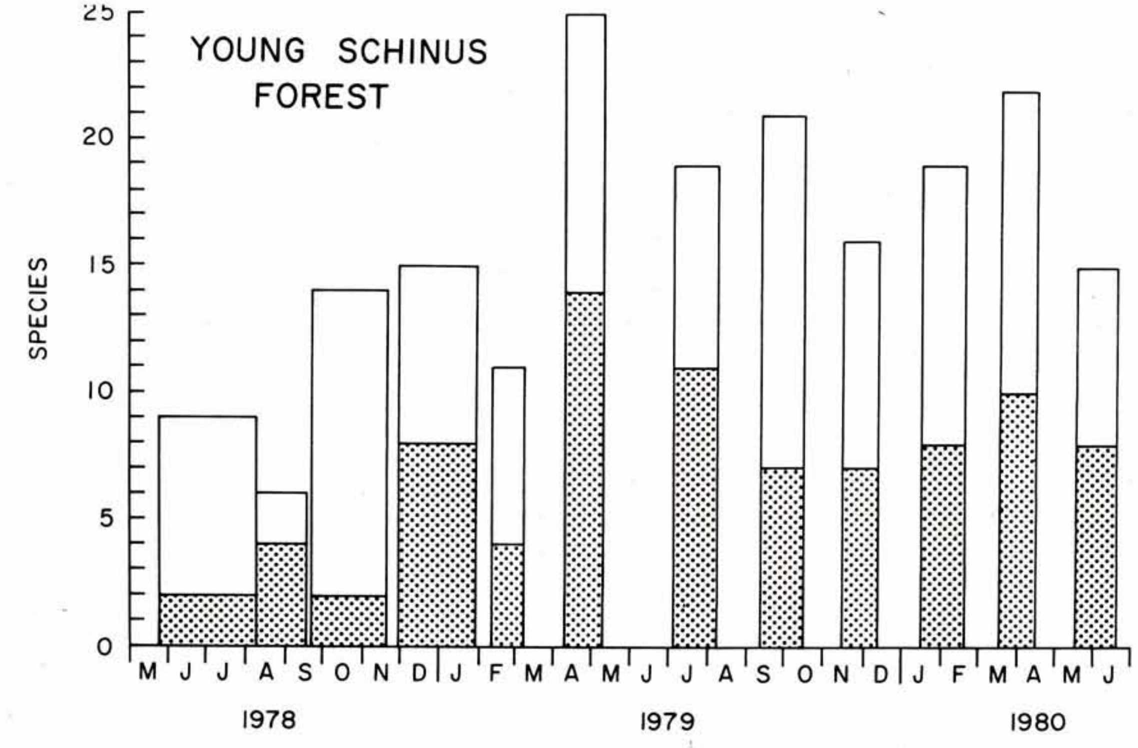


Fig. 37. Continued.



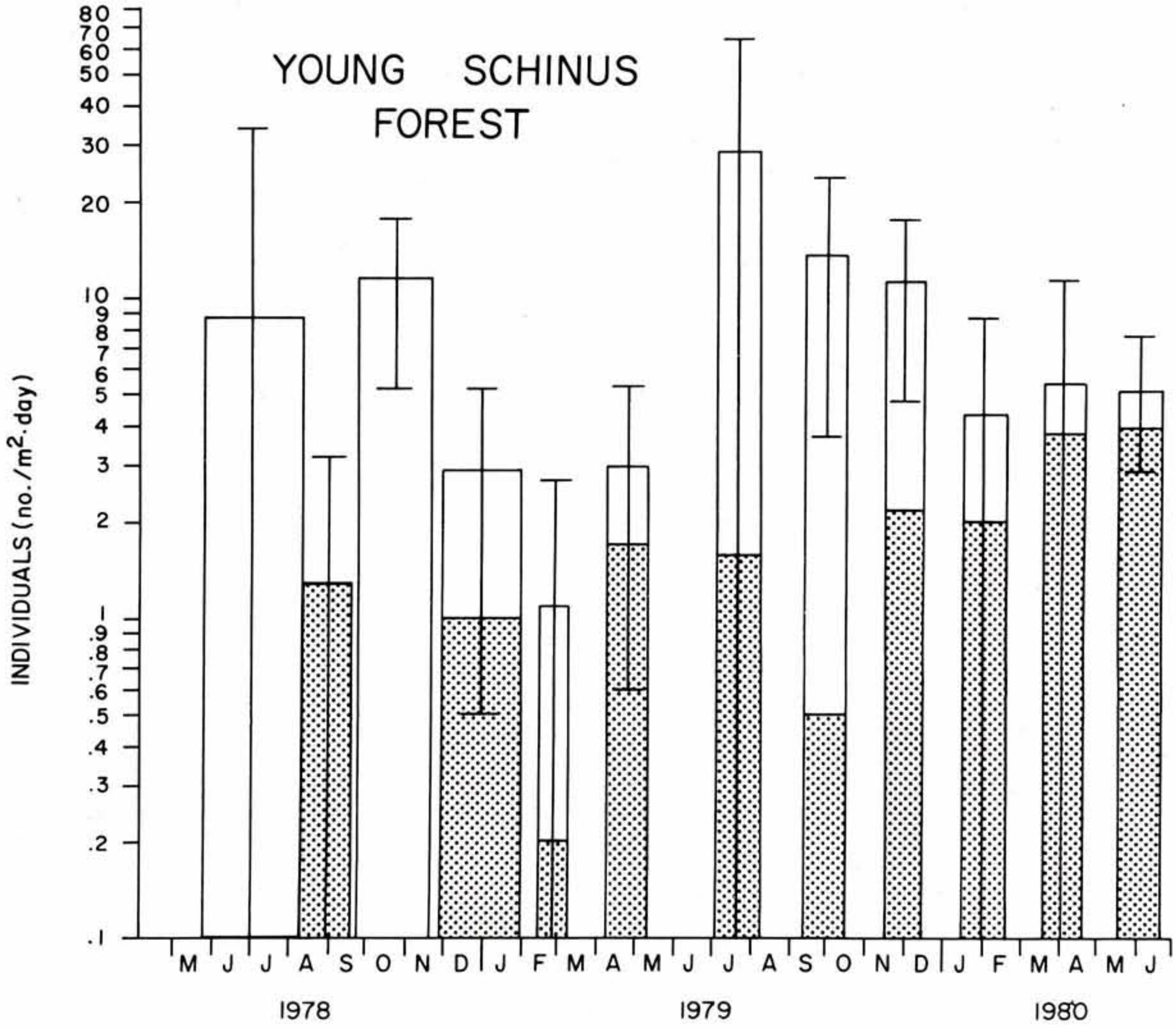


Fig. 37. Continued.

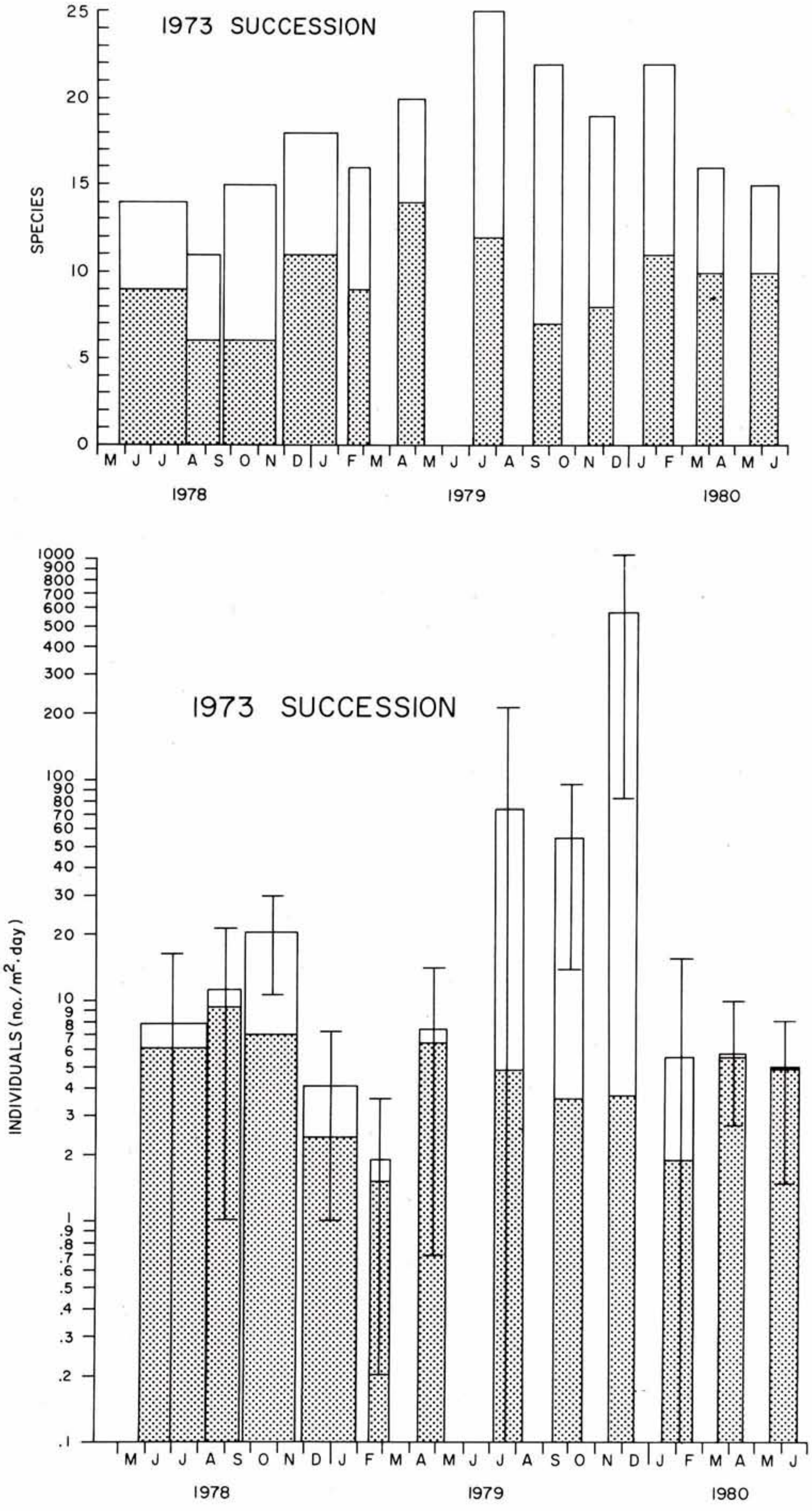
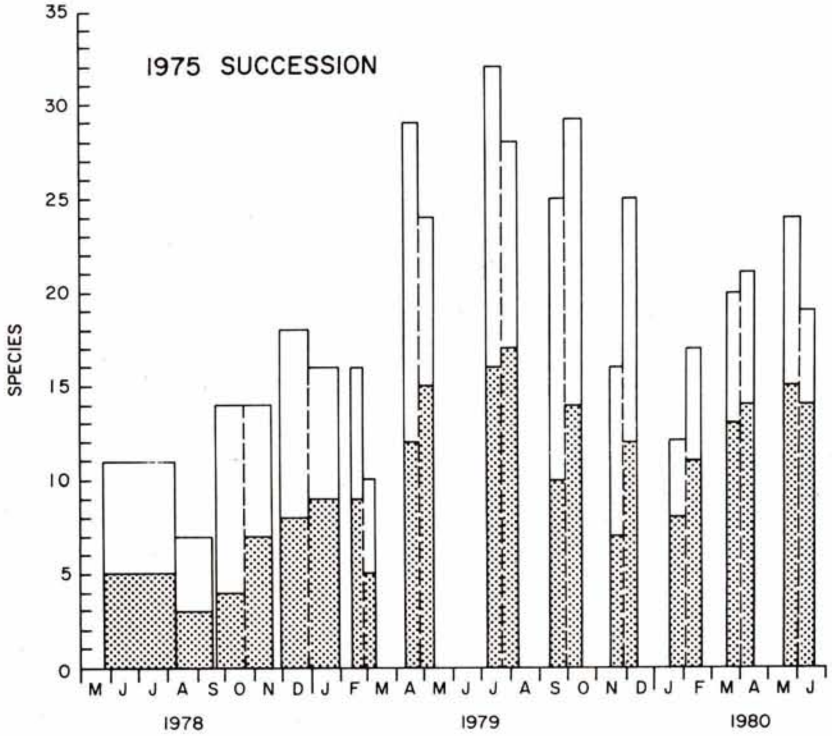


Fig. 37. Continued.



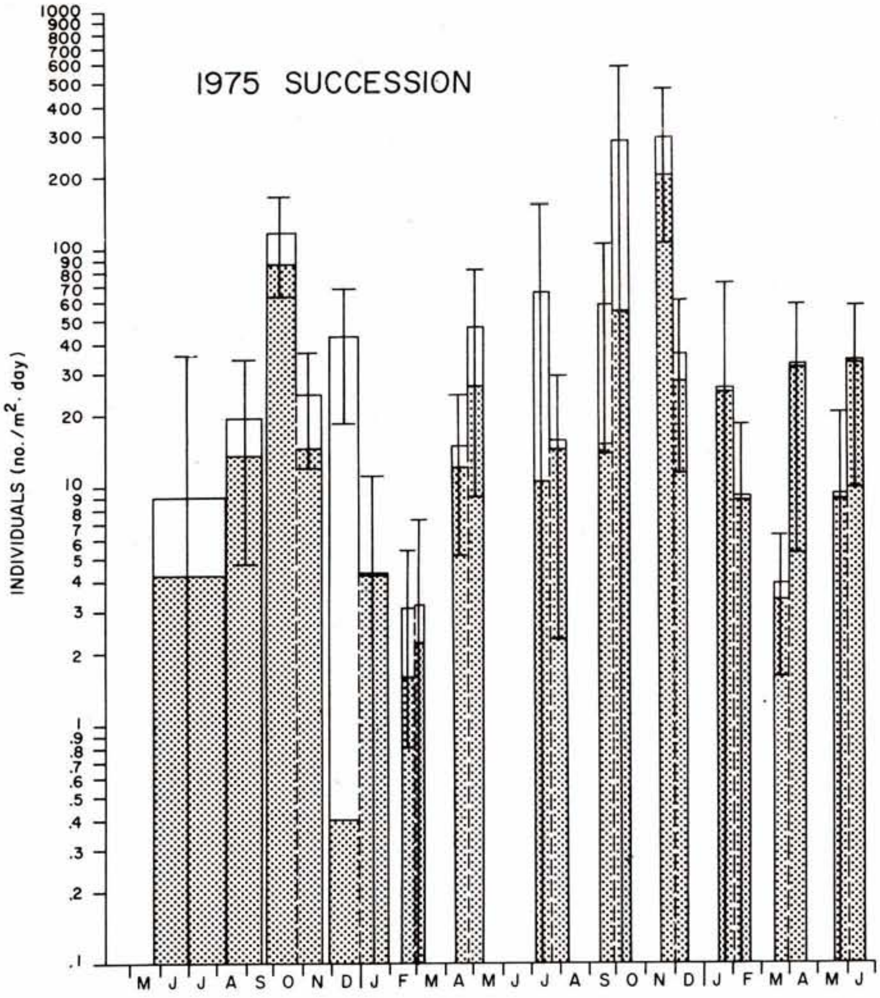


Fig. 37. Continued.

those species do not disperse seeds in the winter. However, mid-winter is precisely the time when schinus, a native of the southern hemisphere, disperses its seeds. It may be exploiting a window when most native species are not dispersing seeds, and therefore may succeed in capturing sites where it might not otherwise be competitive.

Schinus seeds were trapped as early as September and as late as May, and some schinus seeds were trapped at each site where traps were located (Table 28). Although most schinus seeds were trapped in the schinus-dominated forests, a few were captured in the 3 mature communities and still greater numbers were trapped in the young successional vegetations. More schinus seeds were trapped in non-schinus-dominated vegetation during the 1979-1980 fruiting season than during the 1978-1979 fruiting season. This may reflect, in part, the large flocks of robins that moved into the study area during the winter of 1979-1980, compared with the presence of only a few individuals the previous year.

Soil Seed Banks

The seed banks of successional ecosystems are substantially larger than those of mature communities (Table 29). The pineland soil consistently yielded the fewest germinable seeds, and on 1 occasion (Feb. 1979) no seeds germinated from the 4 soil samples taken at that site. The greatest number of plants produced was 28,000 per m^2, from the soil of the old schinus forest no. 1 in July, 1979. However, 95% of those were sporlings of the fern, Thelypteris kunthii. In Nov., 1979, both the 1975 succession and the 1978 bulldozed area yielded $>$11,000 germinable seeds per m^2. Taxa that contributed heavily to those high values included Andropogon glomeratus, Aster subulatus, Boehmeria cylindrica, Brachiaria mutica, Cynoctonum mitreola, Eupatorium coelestinum, Ludwigia octovalvis, Lythrum alatum, Senecio glabella, and Spermacoce assurgens. On any given date, the young successional vegetations tended to have greater soil seed storage than did the older successional vegetation.

The number of species in the soil seed bank ranged from 1 to 29, and the soil of the young successional vegetation yielded more species than that of either the old successional vegetation or the mature communities (Table 30). The seed bank is floristically rich at all seasons, but there tend to be more species present during late summer and early autumn than at other times on most sites.

Schinus germinated from soil samples taken as early as November and as late as April (Table 31). The soil of every site yielded some schinus germination, except the pineland, the 1973 succession, 6 of the 8 Hilsenbeck plots in the 1975 succession, and the 1978 bulldozed area. There is no evidence that schinus retains its viability for many months after it reaches the soil and there is probably little likelihood of schinus germination in soils disturbed during the wet summer months.

Impact of Pineland Burn

The prescribed burn in the pineland had only a modest effect on the seed rain, which increased from 131 to 182 seeds · m^{-2} · day^{-1} after the

Table 28. Schinus seeds trapped. Values are individuals · m^{-2} over period when traps were in field. Each value is a mean from 10 traps (8 in Hilsenbeck plots; 20 in 1973 succession prior to September, 1979, 10 thereafter), each 0.168 m^2. ND = no data.

	May-Aug 1978	Aug-Sept 1978	Sept-Nov 1978	Nov-Jan 1979	Feb-March 1979	April-May 1979	July-Aug 1979	Sept-Oct 1979	Nov-Dec 1979	Jan-Feb 1980	March-April 1980	May - June 1980
MATURE ECOSYSTEMS												
Glade	0	0	0	0.6	0.6	0	0	0	0	1.2	0	0
Pineland	0	0	0	0	0	0	0	0	2.4	2.4	0	0
Hammock	0	0	0	0	0	0	0	0	0	0.6	0	0
OLD SUCCESSIONAL VEGETATION												
Old schinus forest no. 1	0	0	3.0	58.2	20.2	0	0	0	25.6	112.9	3.0	0
Myrica-schinus woodland	0	0	0	40.4	7.7	0	0	0	9.5	64.2	1.8	0
Young schinus forest	0	0	1.2	44.0	4.2	0.6	0	0.6	25.6	55.3	0	0
YOUNG SUCCESSIONAL VEGETATION												
1973 succession	0	0	0	5.1	0	0	0	0	27.9	5.9	0	0
1975 succession												
transect	0	0	0	0	1.2	0	0	0	1.8	1.2	0	0
Hilsenbeck plots	ND	ND	0	6.7	0	0	0	0	0	0	0	0

Table 29. Number of seeds that germinated from soil samples. Values are mean (standard deviation) number of individuals · m^{-2}. All values are based on means of 4 samples, each 130.7 cm^2, with the following exceptions. Hammock means for Feb., June, and Apr., 1980 were based on 8 samples. Means for all sites (except 1975 succession) for Nov., 1978 were based on 5 samples. The 1975 succession values are a combined sampling of the 1975 succession transect plus some or all of the Hilsenbeck plots of the same age, as follows: Nov., 1978 = 5 from transect + 5 each from Hilsenbeck 1, 2, 7, and 8; Feb., 1979 = 5 from transect only; May, 1979 and all dates thereafter = 4 from transect + 4 each from Hilsenbeck 1-8. ND = no data.

	Nov 78	Feb 79	May 79	July 79	Sept 79	Nov 79	Feb 80	April 80	June 80
MATURE ECOSYSTEMS									
Glade	184	249	440	746	77	1,320	478	421	77
	(116)	(296)	(229)	(361)	(62)	(971)	(382)	(202)	(62)
Pineland	77	0	440	459	245	421	19	134	19
	(171)	(0)	(430)	(324)	(201)	(502)	(38)	(158)	(38)
Hammock	92	153	210	402	459	268	143	77	220
	(64)	(165)	(115)	(253)	(324)	(108)	(112)	(91)	(236)
OLD SUCCESSIONAL VEGETATION									
Old schinus forest no. 1	337	172	7,594	28,309	2,429	3,539	593	555	306
	(543)	(170)	(10,176)	(21,775)	(3,080)	(878)	(201)	(169)	(165)
Old schinus forest no. 2	3,198	ND	2,506	ND	ND	ND	ND	ND	ND
	(3,557)		(940)						
Myrica-schinus woodland	367	1,186	670	938	1,377	842	574	784	765
	(232)	(985)	(333)	(855)	(1,900)	(812)	(261)	(315)	(652)
Young schinus forest	2,708	976	3,864	9,143	2,162	3,271	2,199	804	1,129
	(1,774)	(524)	(1,193)	(4,359)	(1,338)	(2,073)	(653)	(469)	(751)
YOUNG SUCCESSIONAL VEGETATION									
1973 Succession	4,024	2,104	3,118	3,347	6,522	5,222	746	1,874	2,602
	(2,774)	(1,305)	(799)	(1,741)	(3,036)	(1,627)	(546)	(867)	(1,149)
1975 Succession	3,100	440	5,515	6,707	5,989	11,413	3,711	2,812	2,527
	(3,308)	(145)	(4,417)	(5,517)	(4,908)	(7,743)	(3,925)	(3,480)	(1,818)
1978 Bulldozed area	1,209	ND	9,717	5,586	5,298	11,228	5,298	4,208	4,762
	(1,352)		(8,351)	(1,370)	(2,024)	(1,701)	(4,425)	(6,080)	(1,687)

Table 30. Number of species germinated from soil samples. Each value is a total of 4 samples, each 130.7 cm^2 (total area of approximately 5.2% of 1 m^2) except Nov., 1978 when 5 samples (total area of approximately 6.5% of 1 m^2) were taken from each site. ND = no data.

	Nov 78	Feb 79	May 79	July 79	Sept 79	Nov 79	Feb 80	Apr 80	June 80
MATURE ECOSYSTEMS									
Glade	7	7	10	10	4	20	10	9	3
Pineland	4	0	10	8	10	9	1	3	1
Hammock, E of road	4	3	7	12	8	7	5	2	5
Hammock, W of road	ND	ND	ND	ND	ND	11	7	2	6
OLD SUCCESSIONAL VEGETATION									
Old schinus forest no. 1	8	7	19	16	17	22	13	12	9
Old schinus forest no. 2	10	ND	19	ND	ND	ND	ND	ND	ND
Myrica-schinus woodland	9	11	13	10	14	14	10	9	9
Young schinus forest	12	9	21	30	14	22	16	9	9
YOUNG SUCCESSIONAL VEGETATION									
1973 Succession	15	15	26	22	21	28	11	16	14
1975 Succession									
Transect	19	9	26	28	19	26	20	16	15
Hilsenbeck plot no. 1	5	ND	10	15	16	9	8	9	9
Hilsenbeck plot no. 2	6	ND	19	13	15	15	7	7	11
Hilsenbeck plot no. 3	ND	ND	16	21	15	25	10	16	13
Hilsenbeck plot no. 4	ND	ND	16	17	16	21	12	10	13
Hilsenbeck plot no. 5	ND	ND	17	23	22	22	14	7	9
Hilsenbeck plot no. 6	ND	ND	16	12	25	19	12	6	11
Hilsenbeck plot no. 7	8	ND	15	28	21	21	14	10	17
Hilsenbeck plot no. 8	8	ND	17	18	21	16	16	17	14
1978 Bulldozed area	9	ND	21	21	23	29	21	22	16

Table 31. Germination of schinus from soil samples. Each value is a mean number of individuals · m^{-2}, based on 4 samples (5 for Nov., 1978) of 130.7 cm^2 each. ND = no data.

	Nov 78	Feb 79	May 79	July 79	Sept 79	Nov 79	Feb 80	Apr 80	June 80
MATURE ECOSYSTEMS									
Glade	0	0	0	0	0	19	0	0	0
Pineland	0	0	0	0	0	0	0	0	0
Hammock, E of road	0	0	0	0	0	57	0	0	0
Hammock, W of road	ND	ND	ND	ND	0	57	0	0	0
OLD SUCCESSIONAL VEGETATION									
Old schinus forest no. 1	0	57	0	0	0	0	77	0	0
Old schinus forest no. 2	0	ND	0	ND	ND	ND	ND	ND	ND
Myrica-schinus woodland	0	153	0	0	0	133	0	0	0
Young schinus forest	0	0	0	0	0	77	115	115	0
YOUNG SUCCESSIONAL VEGETATION									
1973 Succession	0	0	0	0	0	0	0	0	0
1975 Succession									
Transect	0	96	0	0	0	0	0	0	0
Hilsenbeck plot no. 1	0	ND	0	0	0	0	0	0	0
Hilsenbeck plot no. 2	0	ND	0	0	0	0	0	0	0
Hilsenbeck plot no. 3	0	ND	0	0	0	268	0	0	0
Hilsenbeck plot no. 4	0	ND	0	0	0	0	0	0	0
Hilsenbeck plot no. 5	0	ND	0	0	0	19	0	0	0
Hilsenbeck plot no. 6	0	ND	0	0	0	0	0	0	0
Hilsenbeck plot no. 7	0	ND	0	0	0	0	0	0	0
Hilsenbeck plot no. 8	0	ND	0	0	0	0	0	0	0
1978 Bulldozed area	0	ND	0	0	0	0	0	0	0

burn (Table 32). Some of this increase may have been caused by fire-triggered dispersal. The most dramatic effect of the burn was the reduction of the soil seed bank from 421 to 233 seeds · m^{-2}. Considering that the soil seed bank of the pinelands is the most depauperate of any site, this impact on soil seeds may be important in governing post-burn recovery. The increase in post-burn seed-bank species richness (from 9 to 18 species) reflects the greater area of soil sampled after the burn than before.

Seed Floristics

The species germinated from traps or from soil samples are enumerated, by site, in Table 33. The number of taxa (182) enumerated in Table 33 is an underestimate of the actual number because some species (e.g. Baccharis glomeruliflora and B. halimifolia) are indistinguishable as young seedlings, so they are combined in the table. In addition, the seed traps and soil samples yielded some 30 unidentified taxa, and these were not included in Table 33. Weedy species tend to find their way into all sites, whereas species characteristic of the mature communities are not readily dispersed. Most woody species characteristic of the hammock, for example, were not found in traps or soil from other communities. The same was true of characteristic glade species and pineland endemics. The potential for invasion of successional species into mature communities is far greater than is the prospect of recolonization of successional lands by mature-ecosystem species. The seeds of schinus are as ubiquitous as those of any other tree species encountered.

CONCLUSIONS

1. Schinus flowers at the same time--peaking in October--year after year, and all trees flower synchronously. About 10% of the trees flower a second time, in April-May. About 1% of the trees never flower, but another 1% bear male flowers and fruits. Schinus is insect pollinated, and the main pollinator is a syrphid fly, Palpada vinetorum. Fruit set is high; about 35% of the female flowers produce fruits.

2. Most schinus fruits ripen Dec.-Feb. Its seeds are dispersed by animals, but some dispersal is by gravity and some is by water. Opossums, raccoons, catbirds, and robins disperse schinus. Of these, robins are the most important dispersal agent, but large flocks of robins do not visit the study area each year. Schinus seed dispersal is patchy, not uniform. There is year-round production of seeds of many species other than schinus in the study area, but seed production declines in mid-winter. This is precisely the time when the seeds of schinus (a southern hemisphere species) are dispersed, so schinus may be exploiting a colonization time when there is little competition from native species. Schinus gets dispersed to all sites in the study area, and its seeds are moved as far and as abundantly as those of any other tree species studied.

3. The viability of schinus seed is 30 to 60%. Schinus germination is enhanced by scarification with dilute acid, analogous to the conditions that might characterize the digestive tract of some of its

Table 32. Impact of prescribed pineland burn on seed rain and soil seed bank. Seed bank samples were 130.7 cm^2; 4 were taken before burn and 20 after. Seeds were trapped in 10 trays before and after burn; each was 1,683 cm^2.

	Seeds trapped ($no. \cdot m^{-2} \cdot 30\ day^{-1}$)		Soil seed bank ($no. \cdot m^{-2}$)	
	Before/during/ after burn	After burn	Before burn	After burn
1. *Andropogon glomeratus*	1.3			
2. *Baccharis* spp.	46.2	1.6		7.7
3. *Blechum brownei*		7.9	19.1	
4. *Brachiaria mutica*				3.8
5. *Chamaesyce hirta*		0.5		
6. *Chamaesyce hypericifolia*		162.5		34.4
7. *Chamaesyce pinetorum*				7.7
8. *Conyza canadensis*			19.1	
9. *Cynoctonum mitreola*			248.7	
10. *Dyschoriste oblongifolia*				3.8
11. *Erechtites hieracifolia*		0.5		
12. *Erigeron quercifolius*			19.1	
13. *Eupatorium capillifolium*	0.7			
14. *Eupatorium coelestinum*				3.8
15. *Eupatorium leptophyllum*			38.2	
16. *Ficus* sp.				34.4
17. *Launea itybacea*		0.5		
18. *Lepidium virginicum*	1.3			
19. *Ludwigia octovalvis*	0.7	0.5	19.1	
20. *Ludwigia peruviana*		0.5		
21. *Lythrum alatum*		0.5		
22. *Mikania scandens*				38.3
23. *Morinda royoc*				7.7
24. *Myrica cerifera*	0.7	3.1		3.8
25. *Oxalis stricta*				38.3
26. *Paspalum setaceum*			19.1	

Table 32. Continued.

	Seeds trapped (no. · m^{-2} · 30 day^{-1})		Soil seed bank (no. · m^{-2})	
	Before/during/ after burn	After burn	Before burn	After burn
27. *Phyllanthus caroliniensis*				26.8
28. *Pityrogramma trifoliata*	73.3			
29. *Pluchea odorata*		0.5		
30. *Poinsettia pinetorum*				3.8
31. *Portulaca oleracea*		0.5		
32. *Pteris vittata*	1.3			
33. *Rhus copallina*				3.8
34. *Salix caroliniana*	0.7			
35. *Schinus terebinthifolius*	2.6			3.8
36. *Senecio glabellus*		0.5		
37. *Sesbania macrocarpa*	0.7			
38. *Setaria geniculata*				3.8
39. *Solanum americanum*				3.8
40. *Sonchus oleraceus*		1.6		3.8
41. *Thelypteris kunthii*	2.0			
42. *Typha* sp.			19.1	
43. *Youngia japonica*		0.5		
44. Unknown #681			19.1	
Total	131	182	421	233
Number of species	12	15	9	18

Table 33. Plant species germinated from seed traps (T) or soil samples (S) in 11 plant communities. In addition to the 181 taxa enumerated, there were 30 unidentified types. Taxa preceded by W are weedy colonizers of disturbed sites; those preceded by E are exotic species. No trapping was done in the 1978 bulldozed area.

		Mature Ecosystems			Old Successional Vegetation				Young Successional Vegetation			
										1975 Succession		
		Glade	Pine-land	Ham-mock	Old schinus forest no. 1	Old schinus forest no. 2	*Myrica*-schinus wood-land	Young schinus forest	1973 Succession	Transect	Hilsenbeck plots	1978 Bull-dozed
	Acalypha chamaedrifolia		S									
	Aeschynomene sp.			S			T		T			
	Aletris sp.	S										
W	*Alternanthera philoxeroides*				S				T, S	T, S	T, S	
W	*Amaranthus hybridus*						T	S		S	S	
W	*Ambrosia artemisiifolia*	T	T	T	T		T, S	T	T, S	T, S	T, S	
	Ammannia coccinea				T, S			T, S	S	S	S	S
	A. latifolia	T			T, S			T, S	T, S	T, S	S	S
	Ampelopsis arborea									T	S	
	Andropogon glomeratus	T, S		T, S	T, S		T	T, S	T, S	T, S	T, S	S
	Andropogon sp.	T		T	T			T	T		T	
	Anemia adiantifolia	T	T	T	T, S		T, S	T	T, S	T		
E,W	*Ardisia solanacea*									T		

Table 33. Continued.

	Mature Ecosystems			Old Successional Vegetation				Young Successional Vegetation			
									1975 Succession		
	Glade	Pine-land	Ham-mock	Old schinus forest no. 1	Old schinus forest no. 2	*Myrica*-schinus wood-land	Young schinus forest	1973 Succession	Transect	Hilsenbeck plots	1978 Bull-dozed
Aster subulatus	T	T	T	T		T	T, S	T	T	T, S	
Baccharis spp.	T, S	T, S	T, S	T,	S S	T, S	T, S	T, S	T, S	T, S	S
W *Bidens alba*	T	T, S	T	T, S		T, S	T, S	T	T	T, S	
Blechnum serrulatum			T	T			T				
E,W *Blechum brownei*	T, S	T, S	T, S	T, S		T, S	T, S	T	T, S	T, S	S
Boehmeria cylindrica	T, S	T	T	T, S	S	T	T, S	T, S	T, S	T, S	S
E,W *Brachiara mutica*	S		T	T, S		T	T, S	T, S	T, S	T, S	S
Bursera simaruba			T								
Callicarpa americana						S					
Caperonia palustris								T			
E,W *Cardamine pensylvanica*		T									
Cassia deeringiana		T	S								
W *Centella asiatica*	S										S

Table 33. Continued.

	Mature Ecosystems			Old Successional Vegetation				Young Successional Vegetation			
									1975 Succession		
	Glade	Pine-land	Ham-mock	Old schinus forest no. 1	Old schinus forest no. 2	*Myrica*-schinus wood-land	Young schinus forest	1973 Succession	Transect	Hilsenbeck plots	1978 Bull-dozed
W *Chamaesyce hirta*	T, S	T, S	T, S	T, S		T, S	T, S	T, S	T, S	T, S	S
W *C. hypericifolia*	T, S	T, S	T, S	T, S		T, S	T, S	T, S	T, S	T, S	S
W *C. hyssopifolia*						S				T, S	
C. pinetorum		T, S				T					
E,W *Chenopodium album*		T					S	S	S	S	
Chiococca alba									T		
C. parvifolia		S									
Cissus sicyoides				S						S	
E,W *Colocasia esculenta*									T, S	S	
W *Commelina diffusa*	T	T	T, S	T, S			T	T, S	T, S	T, S	S
C. elegans			T								
W *Conobea multifida*				T							
W *Conzya canadensis*		T, S		T		T	T	T	T	T, S	

Table 33. Continued.

		Mature Ecosystems			Old Successional Vegetation				Young Successional Vegetation			
										1975 Succession		
		Glade	Pine-land	Ham-mock	Old schinus forest no. 1	Old schinus forest no. 2	Myrica-schinus wood-land	Young schinus forest	1973 Succession	Transect	Hilsenbeck plots	1978 Bull-dozed
W	Conyza sp.	T, S	T	T	T		T, S	T	T	T		
	Crotalaria pumila		S									
	Cynoctonum mitreola	T, S	T, S		T, S	S	S	T, S	T, S	T, S	T, S	S
E,W	Cynodon dactylon			T				S		T	S	S
E	Cyperus brevifolius		S				S	T, S	S	T	T, S	S
	C. compressus										S	
	C. distinctus		T					S	T	T	S	
	C. haspan	T, S									S	S
	C. surinamensis	T	T	T			T, S	T, S	T, S	T, S	T, S	S
	Cyperus spp.	T	T	T	T		S	T, S	T, S	T, S	T, S	S
	Desmodium canum	T	T, S	T			T	T	T	T	T, S	S
	Dichanthelium aciculare	S										
	D. dichotomum	S								S	S	S
	Dichromena colorata	T, S	S	T	T		S	T, S	T, S	T, S	T, S	S

Table 33. Continued.

		Mature Ecosystems			Old Successional Vegetation				Young Successional Vegetation			
										1975 Succession		
		Glade	Pine-land	Ham-mock	Old schinus forest no. 1	Old schinus forest no. 2	*Myrica*-schinus wood-land	Young schinus forest	1973 Succession	Transect	Hilsenbeck plots	1978 Bull-dozed
	Diodia virginiana					S		T	T, S	S	T, S	
	Dodonaea viscosa		T	T					T			
W	*Dyschoriste oblongifolia*		T, S									
W	*Eclipta prostrata*	T, S		T	T		T	T, S	T, S	T, S	S	S
W	*Eleocharis caribaea*				T			T				S
	Eleocharis sp.	T										
E,W	*Eleusine indica*	T	T	T	T		T	T, S	T, S		T, S	
	Eragrostis elliottii	T										
	Eragrostis sp.	S										
W	*Erechtites hieracifolia*	T, S	T	T	T, S	S	T, S	T, S	T, S	T, S	T, S	
W	*Erigeron quercifolius*	T, S	S				S	S	T	S	T	S
	Erigeron sp.							T				
	Eugenia axillaris		T									
W	*Eupatorium capillifolium*		T, S	S	T, S	S	T, S	T	T, S	T, S	T, S	S

Table 33. Continued.

		Mature Ecosystems			Old Successional Vegetation				Young Successional Vegetation			
										1975 Succession		
		Glade	Pine-land	Ham-mock	Old schinus forest no. 1	Old schinus forest no. 2	*Myrica*-schinus wood-land	Young schinus forest	1973 Succession	Transect	Hilsenbeck plots	1978 Bull-dozed
	E. coelestinum	T	T	S			T	S	T, S	T, S	S	S
W	*E. leptophyllum*	T	T, S	S			S		T	T, S	S	
	Eustachys glauca	T, S	T, S	T, S	T, S		T, S	T, S	T, S	T, S	T, S	S
	Exothea paniculata			T								
	Ficus sp.		T, S	T, S	T	S			T, S	T, S	T, S	S
	Fimbristylis sp.							T				
	Galium hispidulum									S		
	G. obtusum	T			T, S	S		T, S	T, S	T, S	S	S
W	*Geranium carolinianum*			T	T		T	T		S	S	
	Hedyotis nigricans		S									
E	*Heliotropium polyphyllum*	S										S
	Hydrocotyle spp.			T		S				S		S
	Hypericum hypericoides				S							S
	Hyptis alata	T			S						S	S
	Ilex cassine				T, S			T			T, S	
W	*Ipomoea indica*	T			T						T, S	

Table 33. Continued.

	Mature Ecosystems			Old Successional Vegetation				Young Successional Vegetation			
									1975 Succession		
	Glade	Pineland	Hammock	Old schinus forest no. 1	Old schinus forest no. 2	*Myrica*-schinus woodland	Young schinus forest	1973 Succession	Transect	Hilsenbeck plots	1978 Bulldozed
W *I. trichocarpa*	T	T	T			T	T	T	T	T, S	
Juncus megacephalus	T										
Kosteletzkya virginica				T, S			T			S	S
E,W *Lactuca intybacea*									T	S	
E,W *Launaea intybacea*		T	T, S	T		T, S	T	T, S	T	T, S	S
W *Lepidium virginicum*		T						S		T, S	
W *Lepidium* sp.						T					
Ludwigia microcarpa	T, S			T, S			S	T, S	T	T, S	S
W *L. octovalvis*	T, S	T, S	T, S	T, S	S	T, S	T, S	T, S	T, S	T, S	S
W *L. peruviana*	T	T	T	T, S	S	T, S	T, S	T, S	T, S	T, S	S
W *Ludwigia* spp.							T		T		
Lythrum alatum	T, S	T	T	T, S		T, S	T, S	T, S	T, S	T, S	S
E,W *Macroptilium lathyroides*	T	T	T	T		T	T	T	T, S	T	
Mariscus ligularis				T		S	T, S	T		S	S

Table 33. Continued.

		Mature Ecosystems			Old Successional Vegetation				Young Successional Vegetation			
										1975 Succession		
		Glade	Pine-land	Ham-mock	Old schinus forest no. 1	Old schinus forest no. 2	Myrica-schinus wood-land	Young schinus forest	1973 Succession	Transect	Hilsenbeck plots	1978 Bull-dozed
	<u>Mecardonia vandellioides</u>	T		T	T		T, S	T, S	T	T, S	T, S	S
E,W	<u>Medicago lupulina</u>				T		T		T, S	T	T, S	
	<u>Melanthera angustifolia</u>	S										
E,W	<u>Melilotus alba</u>			T	T	S	T				T, S	
	<u>Melothria pendula</u>						T		T	T	T, S	
	<u>Mikania scandens</u>	S	S	S		S	T, S	T, S	T, S	T, S	T, S	S
	<u>Muhlenbergia filipes</u>	T, S										
	<u>Myrica cerifera</u>	T	T	T, S	T, S	S	T, S	T, S	T	T, S	T	
E,W	<u>Oxalis stricta</u>	T	T	T, S	T, S		T, S	T, S	T, S	T	T, S	S
	<u>Panicum purpurascens</u>	T, S		T	T		T, S	T	T, S	T, S	T, S	
	<u>Panicum</u> sp.			S						T		
	<u>Parthenocissus quinquefolia</u>			T	T, S		T	T, S				
W	<u>Parietaria floridana</u>						T	S	S	T	S	

Table 33. Continued.

		Mature Ecosystems			Old Successional Vegetation				Young Successional Vegetation			
										1975 Succession		
		Glade	Pine-land	Ham-mock	Old schinus forest no. 1	Old schinus forest no. 2	*Myrica*-schinus wood-land	Young schinus forest	1973 Succession	Transect	Hilsenbeck plots	1978 Bull-dozed
E,W	*Parthenium hysterophorus*	S	S	T, S	S	S			T, S	T, S	T, S	
W	*Paspalum conjugatum*									T	T	
E,W	*P. dilatatum*			T								
	P. setaceum		T									
W	*Paspalum* spp.		T		T			T		T	T	
	Persea borbonia			T	T, S							
W	*Phyla nodiflora*	S			T		S	T, S	T	T, S	T, S	S
W	*Phyllanthus caroliniensis*	S										S
	P. pentaphyllus		T	T								
W	*Phyllanthus* spp.	T	T, S	T	T		T	T, S	T		T, S	
	Pinus elliotti		T, S									
	Piriqueta caroliniana	S	S									S
	Pityrogramma trifoliata	T	T	T	T, S	S	T	T	T	T	T, S	
E,W	*Plantago major*									T		

Table 33. Continued.

	Mature Ecosystems			Old Successional Vegetation				Young Successional Vegetation			
									1975 Succession		
	Glade	Pine-land	Ham-mock	Old schinus forest no. 1	Old schinus forest no. 2	Myrica-schinus wood-land	Young schinus forest	1973 Succession	Transect	Hilsenbeck plots	1978 Bull-dozed
W *Pluchea odorata*	T, S	T, S	T	T		T	T, S	T	T, S	T, S	S
W *P. rosea*			T						T		
Poinsettia pinetorum		S									
Polygonum hydropiperoides									T, S	T, S	
E,W *P. lapathifolium*								T		S	
E,W *Portulaca oleracea*	T	T		T		T, S	S	S	S	S	
E,W *Psidium guajava*		T	S							T	
P. longipes	S	T	T								S
W *Pteris vittata*	T, S	T	T, S	T, S	S	T, S	T	T, S	T	T, S	
W *Pteris* spp.						T					
W *Ptilimnium capillaceum*									T, S		
Pycreus polystachyos	T	T	T	T, S		T, S	T, S	T, S	T, S	T, S	S
P. pumilus						T	T				
Quercus virginiana			T								

Table 33. Continued.

		Mature Ecosystems			Old Successional Vegetation				Young Successional Vegetation			
										1975 Succession		
		Glade	Pine-land	Ham-mock	Old schinus forest no. 1	Old schinus forest no. 2	*Myrica*-schinus wood-land	Young schinus forest	1973 Succession	Transect	Hilsenbeck plots	1978 Bull-dozed
	Rhus copallina			S					T			
E,W	*Rhynchosia minima*		T									
	Rhyncospora divergens	S										S
	R. tracyi	S									S	S
	Rhyncospora sp.	T, S						S				S
W	*Rorippa palustris*				T, S					T	T	
W	*R. teres*								T			
	Sabatia grandiflora	T									S	S
	Salix caroliniana	T	T	T	T		T	T	T	T	T	
	Sarcostemma clausum								T			
E,W	*Schinus terebinthifolius*	T, S	T	T, S	T, S		T, S	T, S	T	T, S	T, S	
W	*Senecio glabellus*	T	T	T, S	T			T	S	T	T S	S
W	*Sesbania macrocarpa*	T	T	T	T			S	T, S	S	S	
W	*Setaria geniculata*	S	T	T, S	T			T		T, S	S	

Table 33. Continued.

		Mature Ecosystems			Old Successional Vegetation				Young Successional Vegetation			
										1975 Succession		
		Glade	Pine-land	Ham-mock	Old schinus forest no. 1	Old schinus forest no. 2	*Myrica*-schinus wood-land	Young schinus forest	1973 Succession	Transect	Hilsenbeck plots	1978 Bull-dozed
W	*Sida acuta*	T, S	T	T, S	T, S		T, S	T, S	T, S	T	T, S	S
W	*S. rhombifolia*	T							T		T, S	
W	*Solanum americanum*				S		T		T, S	S	T, S	S
	S. ottonis	T			T				S	T	T	
	Solidago leavenworthii	T	T	S	T, S			T, S	T, S	T	T, S	
	S. sempervirens							T				
	S. stricta							S	T			
E,W	*Sonchus asper*	T			T		T, S		T	T, S	S	
E,W	*S. oleraceus*	T	T, S	T, S	T, S		T	T	T	T, S	T, S	
W	*Sonchus* spp.							T	T			
	Spermacoce assurgens	T, S	T	T, S	T, S	S	T, S	T, S	T, S	T, S	T, S	S
	S. tenuoir						T, S	T, S	T, S	S	S	S
W	*S. tetraquetra*			S	S		S	S	T, S	S	S	
	Spiranthes vernalis	T										
	Sporobulus sp.									T		
W	*Stachytarpheta jamaicensis*				S			S				
	Tetrazygia bicolor		T, S	S	T		T					

Table 33. Continued.

		Mature Ecosystems			Old Successional Vegetation				Young Successional Vegetation			
										1975 Succession		
		Glade	Pine-land	Ham-mock	Old schinus forest no. 1	Old schinus forest no. 2	*Myrica*-schinus wood-land	Young schinus forest	1973 Succession	Transect	Hilsenbeck plots	1978 Bull-dozed
	Thelypteris kunthii	T, S	T, S	T, S	T, S	S	T	T, S	T, S	T, S	T, S	S
	Torulinium odoratum			T				T	S	S	S	
	Trema micrantha		T	S			S					
	Typha sp.		S									
E,W	*Verbena bonariensis*									S	S	
	V. scabra	T			T, S	S	T	S	S	T, S	T, S	S
E,W	*Vernonia cinerea*								T			
	Vicia acutifolia	T	T	T	T		T	T	T	T	T	S
W	*Vigna luteola*		T, S	T	T		T	T, S	T	T	T	
	Vitis rotundifolia			T, S	T, S		T, S		S		T, S	
E,W	*Waltheria indica*		T					T				
E,W	*Youngia japonica*		T		T			T	S	T, S	S	
E,W	*Zeuxine strateumatica*											S

dispersal agents. The germination of native competitors of schinus, such as Ilex and Myrica, is enhanced by scarification, but is still lower than the per cent germination of schinus. Mechanical or chemical scarification of Myrica is essential for germination. In nature this is probably accomplished by its dispersal agents, such as the tree swallows that visit the study area in huge flocks each year. Broadcast seeding of unscarified Myrica seed is unlikely to lead to successful colonization.

4. Field germination of schinus occurs Nov.-April, but most takes place Jan.-Feb. Germination rates in excess of 100 seedlings per m^2 per 15 days are common in schinus-dominated communities. Schinus seeds can, and do, germinate at all sites in the study area. Germination rates in the field range from 1 to 30%. Germination is greatest in the first month following dispersal, and tapers off thereafter. Schinus seeds do not retain their viability more than 5 mo following dispersal.

5. In schinus forests there are about 10 to >200 schinus seedlings per m^2. Even though the seedling population density rises and falls during the year, there is never a time when there are no seedlings in the understory. Schinus seedlings are remarkably tenacious, and can survive for years in dense shade, where they grow very slowly. In openings, however, schinus seedlings grow very fast. Even seedlings whose growth has been suppressed for years can respond to canopy openings with rapid growth.

6. Once established, schinus seedlings can survive at all sites in the study area. Established seedlings grow fast in most (but not all) young successional communities, and slowly in most (but not all) older communities. Under good growing conditions, schinus can reproduce within 3 yr after germination. About 20% of the schinus seedlings exposed to prescribed pineland fire resprout.

7. Schinus can tolerate a wide range of site conditions, ranging from sites that seldom flood--such as pinelands and hammocks--to sites that are inundated for several months each year, such as wet prairies. Although schinus tolerates a wide range of water levels, seedling mortality increases when water levels change quickly. Manipulation of water regimes may offer one way to reduce schinus seedling numbers. The microsites created during farming are of little importance in influencing schinus invasion, and schinus invasions will not be reduced by levelling the old rows and furrows.

8. Young successional communities are more susceptible to schinus invasion than are old successional communities, and all successional communities are more susceptible than are mature, native communities. Undisturbed pineland is more susceptible to schinus invasion than is undisturbed glade or wet prairie, and hammocks are less susceptible to invasion than are the other two undisturbed ecosystems.

9. Schinus-dominated forests contain 200 to >2500 schinus trees per ha, and each tree has 1.2 to 7.6 stems, each of which must be treated

individually if herbicides are to be applied directly to the bark. This means that 300 to 6000 stems per ha would require treatment if both sexes were to be killed, or half that many if only females were to be killed. The distribution of schinus trees is patchy, and all schinus-dominated forests contain native species. If the native species are left undisturbed the probability of immediate recolonization by schinus following stand treatment will be reduced.

10. A basal application of a low dosage of triclopyr is a safe, effective way to kill individual schinus trees. Foliar applications of glyphosate or triclopyr can be used to kill schinus as well. Foliar applications may be especially well suited for killing understory schinus before opening the canopy of a schinus forest.

11. If canopy female schinus trees are to be killed the understory schinus seedlings must be killed also, or else gap-capture by the understory schinus is inevitable. The management technique of matricide (killing of reproductively mature females) requires that: 1) understory schinus seedlings be killed, 2) canopy male schinus trees not be killed, and 3) at least 2 treatments be applied to the stand.

12. Seed rain and soil seed storage are extremely high in the study area. In mature communities the seed rain consists of <40 seeds per m^2 per day, but in young successional communities the seed rain is >100 (frequently >500) seeds per m^2 per day. The seed input to a mature ecosystem consists of about 20 species per month, whereas the seed flora falling in a successional community is frequently >25 species per month. The number of seeds stored in the soil varies widely, and ranges from 0 to $>10,000$ per m^2. There are more seeds in the soil of successional communities than in the soil of mature ecosystems, and undisturbed pineland has fewer seeds in its soil than does any other community in the study area. Furthermore, prescribed burns in the pineland reduce the soil-seed storage by nearly 50%. The seed bank in the soil at all sites contains 1 to 29 species. Seeds of weedy species get to all sites; seeds of species typical of mature communities (e.g. hammock trees) do not readily get out of their characteristic ecosystems. Thus, ecosystem recovery may be speeded up by seeding and planting.

REFERENCES CITED

Alexander, T. R. 1958. High hammock vegetation of the southern Florida mainland. Quart. J. Fla. Acad. Sci. 21:293-298.

Alexander, T. R. 1967. A tropical hammock on the Miami (Florida) limestone: a twenty-five year study. Ecology 48:863-867.

Alexander, T. R. and A. G. Crook. 1973. Recent and long-term vegetation changes and patterns in South Florida: Part I: Preliminary report. South Florida Environmental Project. University of Miami, Coral Gables, Fla. 224 p. PB-231 939.

Avery, G. N. and L. L. Loope. 1980a. Endemic taxa in the flora of South Florida. South Florida Research Center Report T-558. U. S. National Park Service, Homestead, Fla. 39 p.

Avery, G. N. and L. L. Loope. 1980b. Plants of Everglades National Park: a preliminary checklist of vascular plants. South Florida Research Center Report T-574. U.S. National Park Service, Homestead, Fla. 41 p.

Baker, H. G. 1976. "Mistake" pollination as a reproductive system with special reference to the Caricaceae. Pp. 161-169 in J. Burley and B. T. Syles (eds.). Tropical Trees: Variation, Breeding and Conservation. Linnaean Society of London. Academic Press.

Barkley, F. A. 1944. Schinus L. Brittonia 5:160-198.

Breen, R. 1978. Schinus control experimentation Hole-in-the-Donut 1978. Unpublished Report, Everglades National Park. 17 p.

Campbell, G. R., J. W. Campbell, and A. L. Winterbotham. 1980. The first Fund for Animals, Inc. Schinus terebinthifolius Brazil expedition, July 1980. Interim Report. The Fund for Animals, Inc., Box 655, Sanibel, Fla. 22 p.

Craighead, F. C., Sr. 1971. The trees of South Florida. Vol. 1. The natural environments and their succession. University of Miami Press, Coral Gables, Fla. 212 p.

Craighead, F. C., Sr. 1974. Hammocks of South Floirda. p. 53-60 in P. J. Gleason (ed.). Environments of South Florida: Present and Past. Miami Geol. Soc. Mem. 2.

Davis, J. H. 1943. The natural features of southern Florida, especially the vegetation and the Everglades. Fla. Geol. Surv. Bull. 25. 311 p.

Dunevitz, V. L. and J. J. Ewel. 1981. Allelopathy of wax myrtle (Myrica cerifera) on Schinus terebinthifolius. Fla. Scientist 44:1-13.

Egler, F. E. 1952. Southeast saline Everglades vegetation, Florida, and its management. Vegetatio Acta Geobotanica 3:213-265.

Ewel, J. and L. Conde. 1979. Seeds in soils of former Everglades farmlands. p. 225-234 in R. M. Linn (ed.) Proceedings of the First Conference on Scientific Research in the National Parks, New Orleans, Nov. 9-12, 1976.

Gogue, G. J., C. J. Hurst, and L. Bancroft. 1974. Growth inhibition by Schinus terebinthifolius. Amer. Soc. Hort. Sci. 9:45.

Hilsenbeck, C. 1976a. A comparison of forest sampling methods in hammock vegetation. Unpublished Master's Thesis. University of Miami, Coral Gables, Fla. 92 p.

Hilsenbeck, C. 1976b. An investigation of old field succession in Everglades National Park, First Interim Report. Unpublished Report. Everglades National Park. 63 p.

Koepp, W. P. 1979. The status of Schinus manipulation in Everglades National Park. p. 45-47 in Schinus. Technical Proc. of Techniques for control of Schinus in South Florida: a workshop for area managers. The Sanibel-Captiva Conservation Foundation, Inc., Sanibel, Fla.

Linhart, Y. B. and P. Feinsinger. 1980. Plant-hummingbird interactions: effects of island size and degree of specialization on pollination. J. Ecol. 68:745-760.

Little, E. L., Jr., R. O. Woodbury, and F. H. Wadsworth. 1974. Trees of Puerto Rico and the Virgin Islands. Vol. 2. Agriculture Handbook No. 449. U.S.D.A. Forest Service, Washington, D. C. 1024 p.

Long, R. W. and O. Lakela. 1971. A Flora of Tropical Florida. University of Miami Press, Coral Gables, Fla.

Loope, L. L. and V. L. Dunevitz. 1981a. Impact of fire exclusion and invasion of Schinus terebinthifolius on limestone rockland pine forests of southeastern Florida. South Florida Research Center Report T-645. U.S. National Park Service, Homestead, Fla. 30 p.

Loope, L. L. and V. L. Dunevitz. 1981b. Investigations of early plant succession on abandoned farmland in Everglades National Park. Unpublished Technical Report. South Florida Research Center. U.S. National Park Service, Homestead, Fla.

Meador, R. E. II. 1977. The role of mycorrhizae in influencing succession on abandoned Everglades farmland. Unpublished Master's Thesis. University of Florida, Gainesville. 100 p.

Morton, J. F. 1977. Plants Poisonous to People in Florida and Other Warm Areas. Fairchild Tropical Garden, Miami, Fla. 116 p.

Morton, J. F. 1978. Brazilian pepper--its impact on people, animals and the environment. Econ. Bot. 32:353-359.

Nilsen, E. T. and W. H. Muller. 1980. A comparison of the relative naturalization ability of two Schinus species in southern California. I. Seed germination. Bull. Torrey Bot. Club 107:51-56.

Oliveira, F. and A. Souza Grotta. 1965. Contribucão ao estudo morfológico e anatómico de Schinus terebinthifolius Raddi Anacardiaceae. Rev. Fac. Farm. Bioqium. Sao Paulo 3:271-293.

Olmsted, I. C., L. L. Loope, and C. E. Hilsenbeck. 1980. Tropical hardwood hammocks of the interior of Everglades National Park and Big Cypress National Preserve. South Florida Research Center Report T-604. U.S. National Park Service, Homestead, Fla. 58 p.

Phillipps, W. S. 1940. A tropical hammock on the Miami (Florida) limestone. Ecology 21:166-175.

Resource Management Staff. 1976. Hole-in-the-Donut Farmland Research and Management Program, Summary 1972-1976. Unpublished Report. Everglades National Park. 51 p.

Robertson, W. B., Jr. 1953. A survey of the effects of fire in Everglades National Park. U.S. National Park Service, Homestead, Fla. 75 p.

Robertson, W. B., Jr. 1955. An analysis of the breeding-bird populations of tropical Florida in relation to the vegetation. Unpublished Doctoral Dissertation, University of Illinois, Champaign-Urbana. 599 p.

Salamon, J. 1981. Many gourmets get the itch to sample pink peppercorns. The Wall Street Journal, vol. 198 (121), 21 December.

Stephenson, A. G. 1981. Flower and fruit abortion: proximate causes and ultimate functions. Ann. Rev. Ecol. Syst. 12:253-279.

Tomlinson, P. B. 1980. The Biology of Trees Native to Tropical Florida. P. B. Tomlinson, Harvard Forest, Petersham, MA. 480 p.

USDA. 1958. Soil survey of Dade County, Florida. Series 1147, No. 4. Soil Conservation Service and the University of Florida Agricultural Experiment Station.

Wade, D., J. Ewel, and R. Hofstetter. 1980. Fire in South Florida Ecosystems. U.S.D.A. Forest Service General Technical Report SE-17. Southeastern Forest Experiment Station. Asheville, North Carolina. 125 p.

Woodall, S. 1979a. Physiology of Schinus. p. 23-42 in Schinus. Technical Proc. of Techniques for control of Schinus in South Florida: a workshop for area managers. The Sanibel-Captiva Conservation Foundation, Inc., Sanibel, Fla.

Woodall, S. 1979b. Results of several herbicide screening tests on *Schinus*. p. 63-75 *in Schinus*. Technical Proc. of Techniques for control of *Schinus* in South Florida: a workshop for area managers. The Sanibel-Captiva Conservation Foundation, Inc., Sanibel, Fla.

Workman, R. W. 1979. History of *Schinus* in Florida. p. 5-6 *in Schinus*. Technical Proc. of Techniques for control of *Schinus* in South Florida: a workshop for area managers. The Sanibel-Captiva Conservation Foundation, Inc., Sanibel, Fla.

WSSA. 1979. Herbicide Handbook of the Weed Science Society of America. Fourth Ed. Champaign, Illinois, 479 p.