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The Structural Complexity of Old Field Vegetation and the Recruitment of Bird-Dispersed Plant Species

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Summary. The input of bird-disseminated seeds into four old fields of different structural complexity was examined. Seed input was greatest along the edges of fields. Significantly more seeds were found in a 13 year old field that had structurally complex vegetation, than in a 3-year-old field with a single layer of vegetation. The lower input into the latter field was a function of both low fruit availability and low structural complexity of the field. Similarly, more seeds were found in a 2-year-old field which had artificial structures, simulating saplings, placed in it than in an adjacent control field of the same age. The shape of the structures was not a significant factor in the input of seeds. Timing of seed deposition was correlated with fruit ripening times, relative nutritional value of the fruit and the movements of frugivorous birds. The input of bird-disseminated seeds into fields appears to be directly related to the structural complexity of the vegetation. Woody plants increase the structural complexity of the old fields and serve as recruitment foci for bird-disseminated seeds. Thus, seed deposition by birds influences vegetation pattern, and conversely, the presence of recruitment foci in the vegetation may influence bird dispersal patterns of bird-disseminated seeds.

Introduction

The important role birds play in the dispersal of plant seeds is well documented (Ridley 1930; van der Pijl 1972). In the eastern deciduous forest of North America, over 300 species of plants produce fruits, the seeds of which are dispersed primarily by birds (Stiles 1980; Martin et al. 1951). Many woody species which become established soon after disturbances, such as cultivation and lumbering, are bird-dispersed, e.g. *Cornus florida* L., *Prunus serotina* Ehrh., *Rubus* spp., *Juniperus virginiana* L. and *Rosa* spp. (Bard 1952; Marks 1974; Beckwith 1954; Smith 1940; Auclair and Cottam 1971). There is much circumstantial evidence, but only a few quantitative measurements, of bird-disseminated seed input into disturbed areas (Beckwith 1954; Livingston 1972; Smith 1975). In general, information on the dispersal of bird-disseminated seeds in temperate regions is lacking (Thompson and Willson 1979).

Our study was designed to answer the following questions: 1. What is the input of bird-disseminated seeds into post-agricultural fields? 2. Does this input change with successional increases in structural complexity? 3. How does the forest edge influence seed input? 4. Does artificially increasing the structural complexity of a post-agricultural field affect input of bird-disseminated seeds? and 5. Are any structural types more effective as recruitment foci?

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Structural Complexity of Old Field Vegetation

When a cultivated field in the eastern United States is left fallow it is colonized initially by annual and perennial herbs which form a single layer of vegetation, a single stratum of plants ranging in height from a few centimeters to over a meter (Bard 1952; Bazzaz 1968, 1975; Keever 1950; Smith 1940). Trees and shrubs, which later become established, increase the structural complexity of the vegetation by forming taller patches of woody plants in a matrix of herbaceous species. These patches may serve as recruitment foci for bird-disseminated seeds. These are patches in the environment which, by nature of their structure and composition, are commonly frequented by birds. The greater frequency of birds at these sites increases the density of bird-disseminated seeds under these sites and, to a lesser extent, in the area surrounding these sites.

Recruitment foci may exhibit a variety of structural forms which vary temporally and geographically. Five distinct structural types (i.e. recruitment foci) are found in post-agricultural fields in New Jersey. Using branching pattern and overall growth form these were designated: horizontal, pyramid, vertical, arched and vines, representing such species as *Cornus florida*, *Juniperus virginiana*, *Rosa multiflora* and *Lonicera japonica* respectively.

The Study Area

The study was conducted at the William L. Hutcheson Memorial Forest, located on the Piedmont of New Jersey 14 km west of New Brunswick. It consists of a 28 ha mixed oak forest with adjoining fields in varying stages of succession (Fig. 1). The soil is primarily silt loam derived from the underlying red shale of the Brunswick Formation (Ugolini 1964). Mean annual temperature for the area is 11.7° C ranging from a January average of 0.0° C to a July average of 24.0° C (U.S. Weather Bureau 1959). Average annual precipitation is 112 cm distributed evenly throughout the year (Biel 1958).

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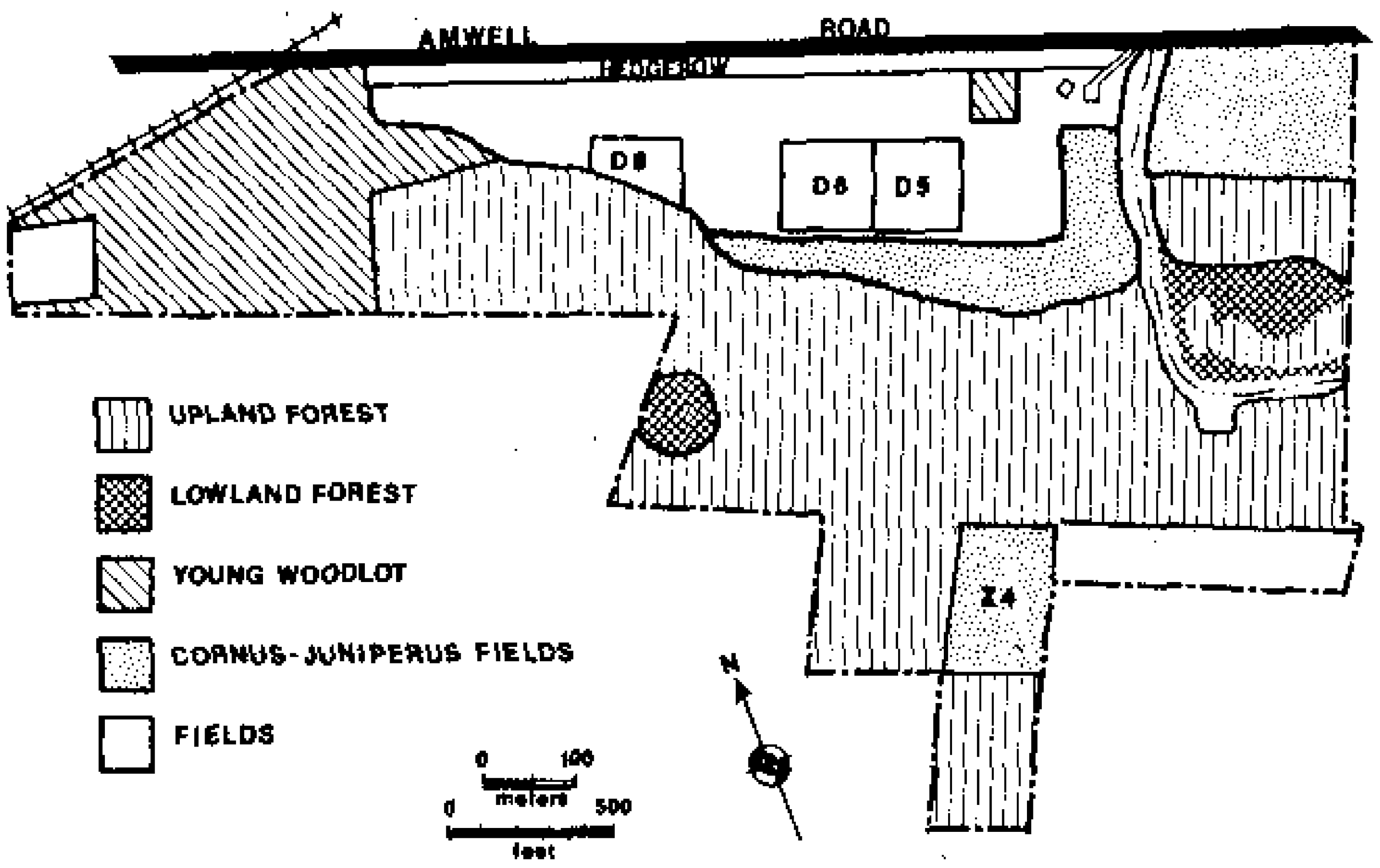

Fig. 1. The location of the study fields at the William L. Hutcheson Memorial Forest, East Millstone, New Jersey

Methods

The input of bird-disseminated seeds was measured using 1 m^2 seed traps modified from a design used by Smith (1975). Traps were constructed of 2.5 × 5.1 cm wood cut and nailed to make a 1 m^2 frame. Six mil polyethylene sheets were cut and stapled to the bottom of the frames. To provide drainage, 10 cm^2 holes were cut in the center of the polyethylene sheets and covered with a fiberglass screen. The screen provided drainage but was small enough to prevent seed loss. Traps were supported on 20 cm wooden legs.

Natural Structural Complexity: Forest Edge and Succession

From July 1977 to March 1978 seed input was measured in two fields, Z-4 and D-8 (Fig. 1). Field Z-4 had been fallow since 1965 and field D-8 had been fallow since 1975. The first seed trap in each field was placed at the forest-field border. The second was placed 5 m from the first in the field and along a line perpendicular to the forest edge. The remaining 9 traps in each field were placed at 10 m intervals along this line. In field Z-4 the line of traps ran parallel to and 10 m from a corn field. Traps were emptied weekly from July 6 to November 21, then every two weeks until snow cover prevented further collections in late December, and finally on March 24 just following snow melt. The structural complexity of the two fields was quite different. The vegetation in field D-8 formed a single layer varying in height 0.5 to 1.2 m, very similar to fields D-5 and D-6 described below. Vegetation in field Z-4 was more complex. In addition to the herbaceous layer at about 1 m, scattered *J. virginiana*, *Rosa multiflora* Thunb. and *C. florida* up to 5 m in height were present. In order to quantify the structural complexity of the vegetation, a 20 m by 90 m transect centered on the line of seed traps was established. The transect was further divided into 10 m^2 quadrats starting from the forest edge (5–15 m) running into the field (85–90 m). The number, height and diameter breast height (dbh) of each woody plant over 1 m tall was recorded for each quadrat (Table 1). There were approximately 8 woody stems greater than 1 m tall per 100 m^2. The density of stems greater than 2 m in height was higher near the forest edge. When the vegetation over 2 m in height was separated by species, 48.6% of the stems were *J. virginiana*, 35.1% were *C. florida* and 16.3% were *R. multiflora* and others.

Artificial Structural Complexity

From September 1980 to March 1981 seed input was measured in two adjacent 1 ha fields, labeled D-5 and D-6 in Fig. 1, which have been fallow since 1978. The fields were covered predominantly by herbs; the dominant species are goldenrods (*Solidago* spp.) and aster (*Aster* spp.). Structural complexities of the vegetation in these two fields were similar to each other and to field D-8. The fields were surrounded by other fields which vary in age since abandonment from 5 to 22 years. Fields to the south and east are part of a long-term old field succession study that began in 1957 (Buell et al. 1971; Small et al. 1971). The fields nearest study plots D-5 and D-6 are dominated primarily by herbaceous species with occasional patches of *J. virginiana*, *R. multiflora* and *Rubus* spp. The fields closer to the forest to the south and to the road to the north have a

Table 1. Density of woody vegetation by height in 10 m × 20 m quadrats along a transect perpendicular to the forest edge and centered on the line of seed traps in Field Z-4. Values given are the number of stems/200 m^2

Quadrat Distance from Forest Edge	Species																			
	Juniperus					*Cornus*				*Rosa*		Other				Total				
	$>1\leq 2$	$>2\leq 3$	$>3\leq 4$	$>4\leq 5$	$>5\leq 6$	$>1\leq 2$	$>2\leq 3$	$>3\leq 4$	$>4\leq 5$	$>1\leq 2$	$>2\leq 3$	$>1\leq 2$	$>2\leq 3$	$>3\leq 4$	$>4\leq 5$	$>1\leq 2$	$>2\leq 3$	$>3\leq 4$	$>4\leq 5$	$>5\leq 6$
5–15	3	1	2	–	–	8	5	1	–	3	4	1	3	3	1	15	13	6	1	–
15–25	2	1	1	3	1	4	7	3	–	4	–	–	–	–	–	10	8	4	3	1
25–35	–	2	1	–	2	3	–	1	1	5	–	1	–	–	–	9	2	2	1	2
35–45	2	1	3	–	–	4	–	1	–	4	–	1	–	–	–	11	1	4	–	–
45–55	1	–	2	1	–	5	–	–	–	–	–	–	–	–	–	6	–	2	1	–
55–65	3	3	4	2	–	2	1	1	–	1	–	1	–	–	–	7	4	5	2	–
65–75	1	1	1	–	1	1	2	–	–	–	–	–	–	–	–	2	3	1	–	1
75–85	–	–	–	–	–	1	2	1	–	–	–	–	–	–	1	1	2	1	1	–
85–95	2	2	1	–	1	1	–	–	–	2	–	2	–	–	–	7	2	1	–	1
Total	14	11	14	6	5	29	17	8	1	19	4	6	3	3	2	68	35	25	9	5

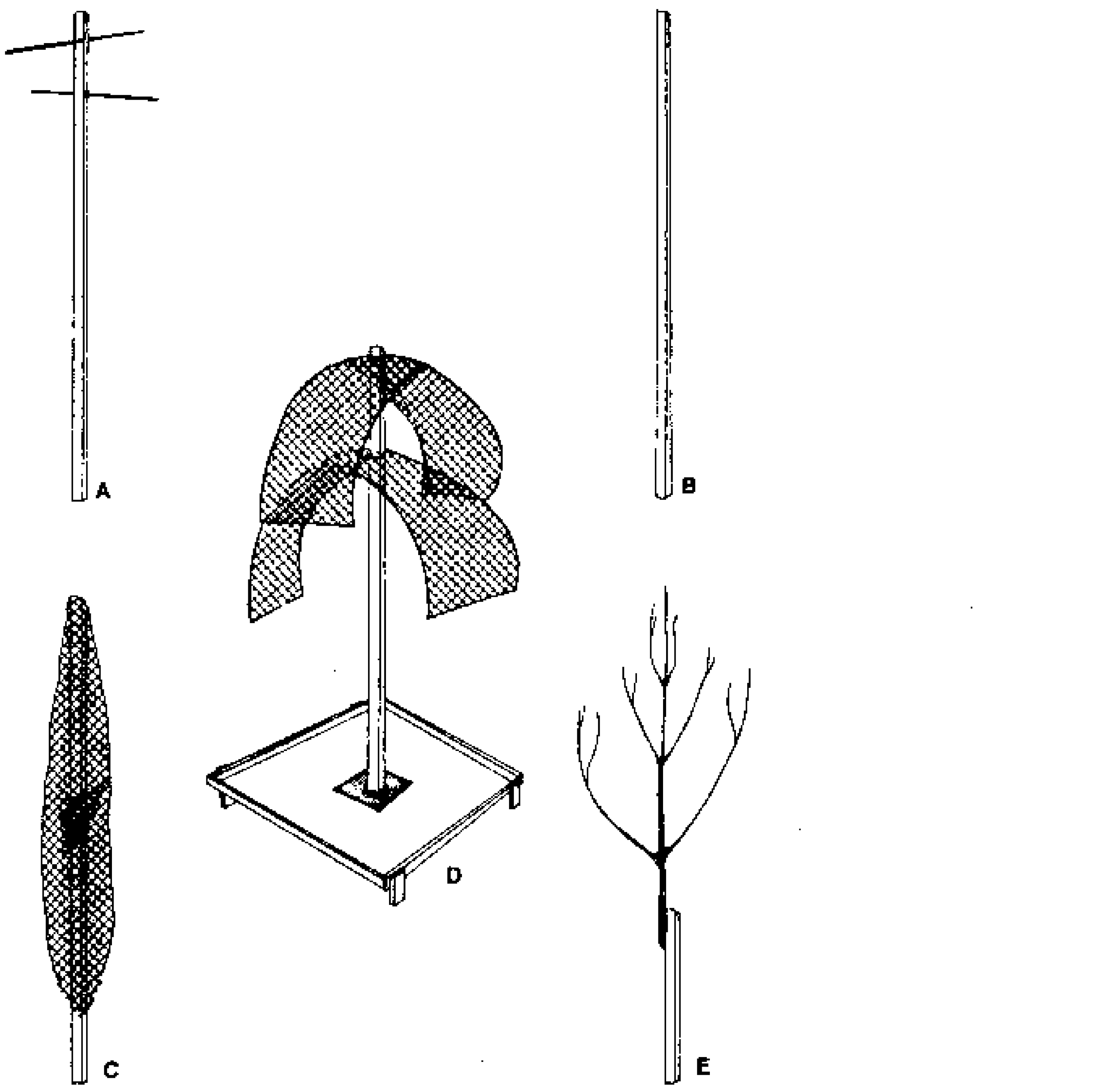

Fig. 2 A–E. Types of artificial structures used: **A** horizontal, **B** vertical, **C** pyramid, **D** arched with seed trap underneath and **E** real plant

much greater concentration of small trees, shrubs and vines due their greater age. Both fields D-5 and D-6 are approximately the same distance from all available species of bird-disseminated plants within 200 m.

Field D-5 was chosen randomly to have its structural complexity increased by artificial structures and real plants. Artificial structures 2 m high were constructed to represent four of the basic structural types; horizontal, pyramid, vertical and arched (Fig. 2).

To test bird response to real plants, 5 year old nursery grown *Acer rubrum* L. stems were cut off at the base and attached to wood posts to reach a height of 2 meters. All structures were supported by 30.5 × 3.8 cm plastic pipe set into the ground. Seed traps were placed under each structure to catch any incoming seeds. Each trap placed under a structure had a 5.1 cm diameter plastic ring sewn into the center of the fiberglass screen to facilitate the placement of the traps directly under the structures. Field D-6 served as the control and contained only 10 seed traps.

Field D-5 contained 6 real plants, 6 seed traps without structures and 6 each of the 4 structural types. They were arranged in a latin square design 10 m apart so that each treatment, e.g. structure type or no structure, occurred once in each row and each column. This was to account for position effect. Ten seed traps were located randomly on a similar grid in the control field (D-6). Seeds were collected from each trap every 2 to 3 days from September 13 to December 31, 1980 and weekly until March 31, 1981. The data from field D-5 were pooled and compared to field D-6 to determine what effect, if any, increasing the structural complexity of the field had on the input of bird-dispersed seeds. The data from field D-5 were also analyzed separately to determine what effect structural type had on seed input.

In addition to using the number of droppings and seeds under each structure, observations were made of bird activity in the field during fall migration (September–November 1980).

Results

Natural Structural Complexity: Forest Edge and Succession

Seeds were collected from traps placed in fields D-8 and Z-4 (henceforth referred to as the simple and complex field respectively) from July 7, 1977 through March 16, 1978. A total of 770 bird-disseminated seeds were collected from the 11 traps in the complex field and 208 seeds were collected from the 11 traps in the simple field (Table 2). The seed input into the fields was tested using analysis of variance techniques (Table 3). The total numbers of seeds collected from the two fields were significantly different whether seeds from the traps along the forest edge were included ($P<0.05$) or excluded ($P<0.01$).

Table 2. Seeds collected in fields Z-4 and D-8 at the William L. Hutcheson Memorial Forest from July 7, 1977 to March 16, 1978

Species	Field Z-4			Field D-8		
	All traps	Without edge trap		All traps	Without edge trap	
	$n=11$	$n=10$	seeds/m^2	$n=11$	$n=10$	seeds/m^2
Rosa multiflora	66	49	4.9	113	50	5.0
Juniperus virginiana	389	344	34.4	13	10	1.0
Lonicera japonica	1	1	0.1	–	–	–
Phytolacca americana	32	20	2.0	–	–	–
Cornus florida	95	60	6.0	8	0	0
Toxicodendron radicans	48	4	0.4	6	5	0.5
Prunus serotina	24	3	0.3	10	1	0.1
Rubus spp.	14	10	1.0	50	0	0
Vitis spp.	49	38	3.3	6	6	0.6
Cornus amomum	2	1	0.1	–	–	–
Viburnum prunifolium	1	1	0.1	–	–	–
Rhus spp.	2	1	0.1	1	1	0.1
Smilacina racemosa	–	–	–	1	1	0.1
	770	532	53.2	208	74	7.4

Table 3. Analysis of variance table for seed input into Fields Z-4 and D-8

Source of variation	All traps ($n=11$)				Without edge traps ($n=10$)				Without edge traps All seeds except *Juniperus virginiana*			
	df	SS	MS	F	df	SS	MS	F	df	SS	MS	F
Total	21	50,476			19	18,196			19	2,334		
Treatment (between fields)	1	14,356	14,356	7.9*	1	12,751	12,751	42**	1	594	595	6.1*
Error	20	36,120			18	5,445	302		18	1,740	97	

* Significant at alpha = 0.05
** Significant at alpha = 0.01

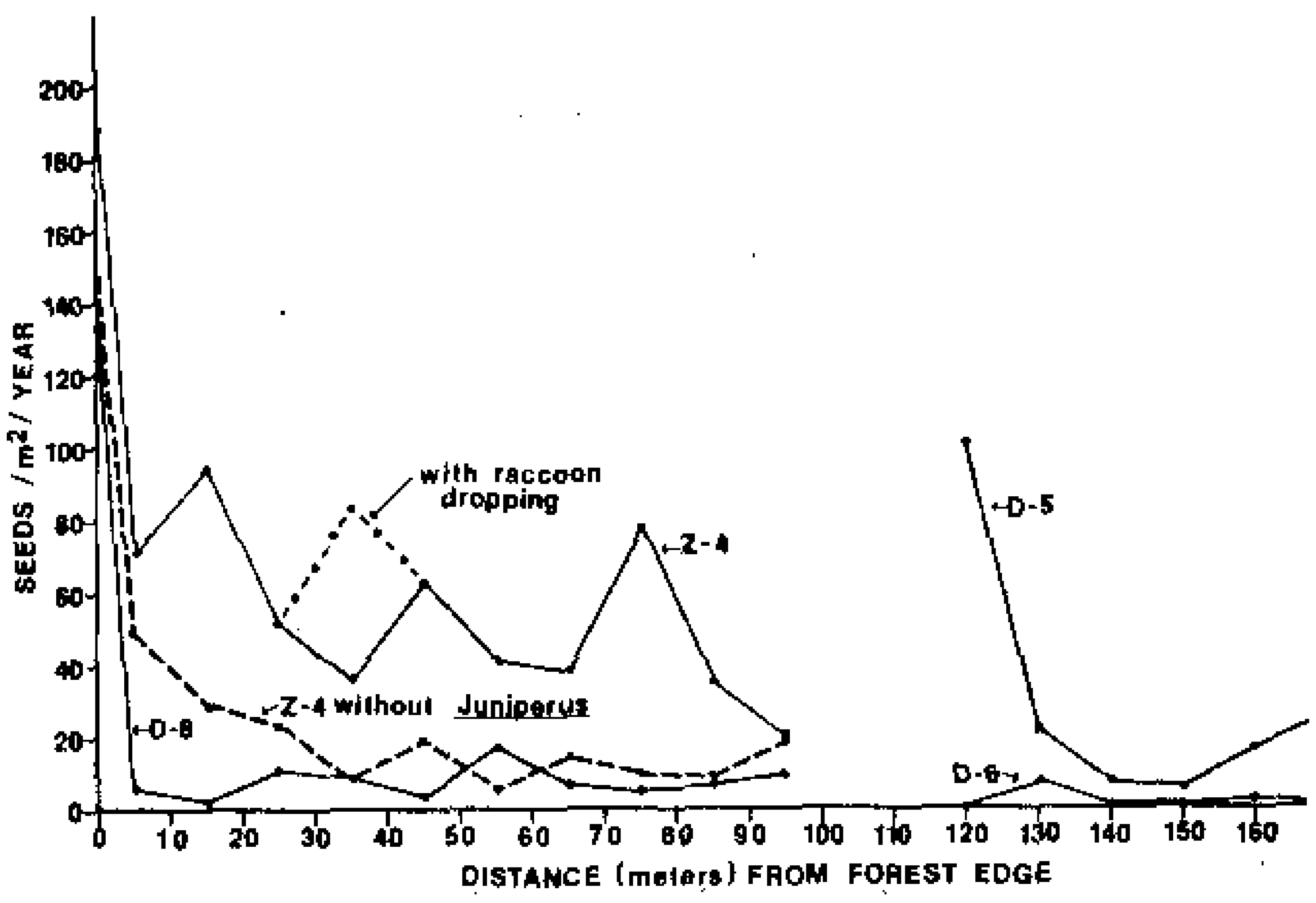

Fig. 3. Bird-dispersed seed input into the study fields as a function of the distance from forest edge

Major seed input in the complex field came from *Juniperus virginiana* (64.7%), *Cornus florida* Ehrh. (11.3%), *Rosa multiflora* (9.2%), and *Vitis* spp. (7.1%) (Table 2). In the simple field the major seed input came from *Rosa multiflora* (69%) and *Juniperus virginiana* (12%). Excluding the trap closest to the forest edge the mean number of bird-disseminated seeds deposited per meter square of trap surface was 53.2 for the complex field and 7.4 for the simple field.

The rate of seed deposition near the forest edge was much greater in both fields (D-8 and Z-4) (Fig. 3). The value for the edge trap in the simple field is elevated due to 47 seeds of *Rubus* sp. which were deposited in one dropping in July. The only other unusual value was 48 *Prunus serotina* seeds deposited in the trap 35 meters from the edge of the complex field. This was probably from a raccoon that defecated in the trap and these seeds were eliminated

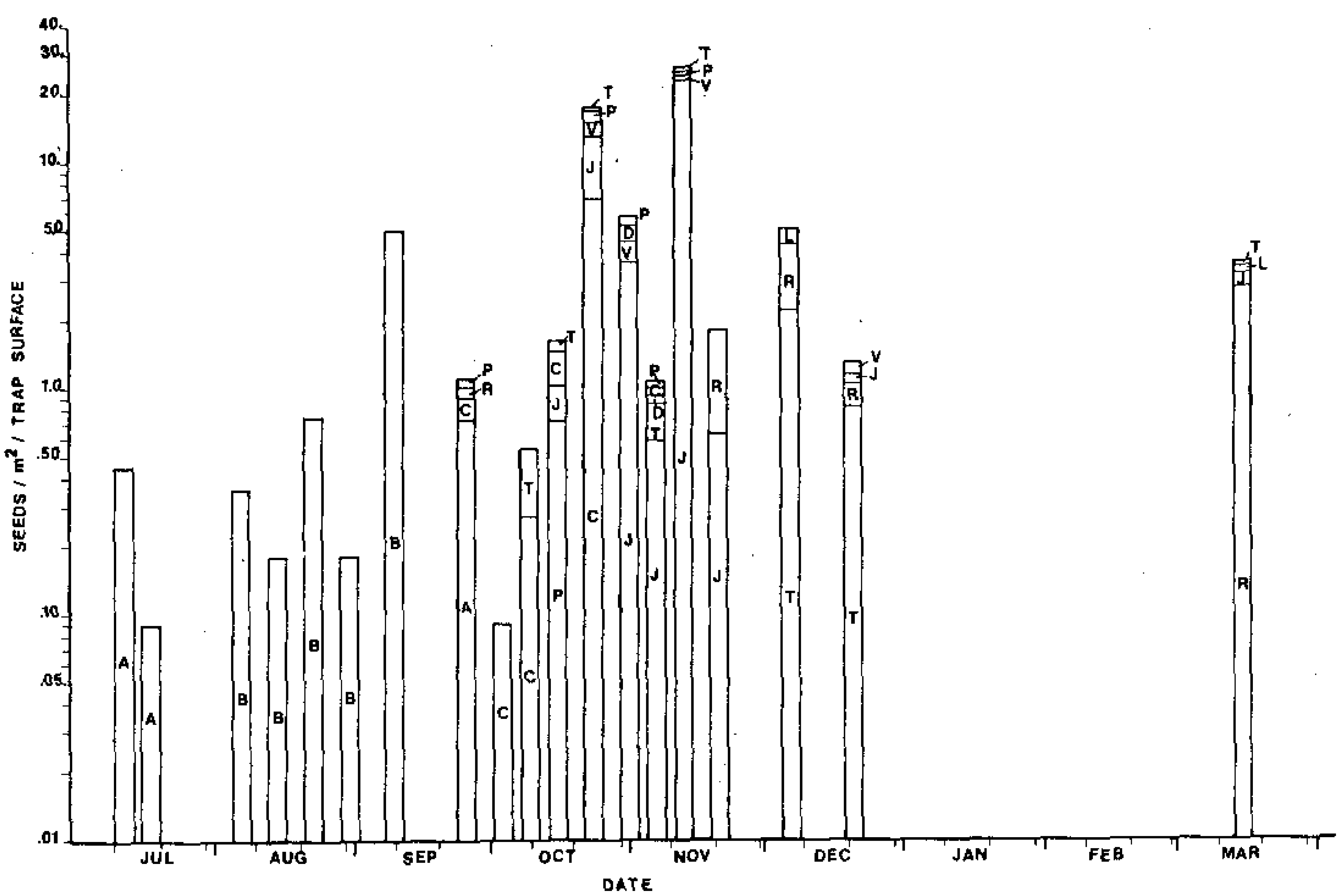

Fig. 4. Input of bird-dispersed seeds into field Z-4 from July 1977 to March 1978. The vertical axis is a log scale. Key: *A*, *Rubus* sp.; *B*, *Prunus* sp.; *C*, *virginiana*; *L*, *Lonicera japonica*; *P*, *Phytolacca americana*; *R*, *Rosa multiflora*, *T*, *Toxicodendron radicans* and *V*, *Vitis* sp.

Table 4. Seeds collected in fields D-5 and D-6 at the William L. Hutcheson Memorial Forest from September 13, 1980 to March 31, 1981

Species	Field D-5								Field D-6	
	Type of structure						Total Seeds	Seeds/m²	Total Seeds	Seeds/m²
	H[a] $n=6$	*P* $n=6$	*V* $n=6$	*A* $n=6$	*R* $n=6$	*T* $n=6$	$n=36$		$n=10$	$n=10$
Rosa multiflora	156	151	61	76	476	59	979	27.1	0	0
Juniperus virginiana	2	6	3	4	19	0	34	0.94	4	0.4
Lonicera japonica	9	4	1	1	11	0	26	0.72	0	0
Phytolacca americana	0	0	4	1	0	1	6	0.17	7	0.7
unknown	0	0	0	6	0	0	6	0.17	0	0
Total	167	161	69	88	506	60	1,051		11	
Seeds/m²	27.8	26.8	11.5	14.6	84.3	10	29.1		1.1	

[a] Key: H = horizontal, P = pyramid, V = vertical, A = arched, R = real plant and T = no structure

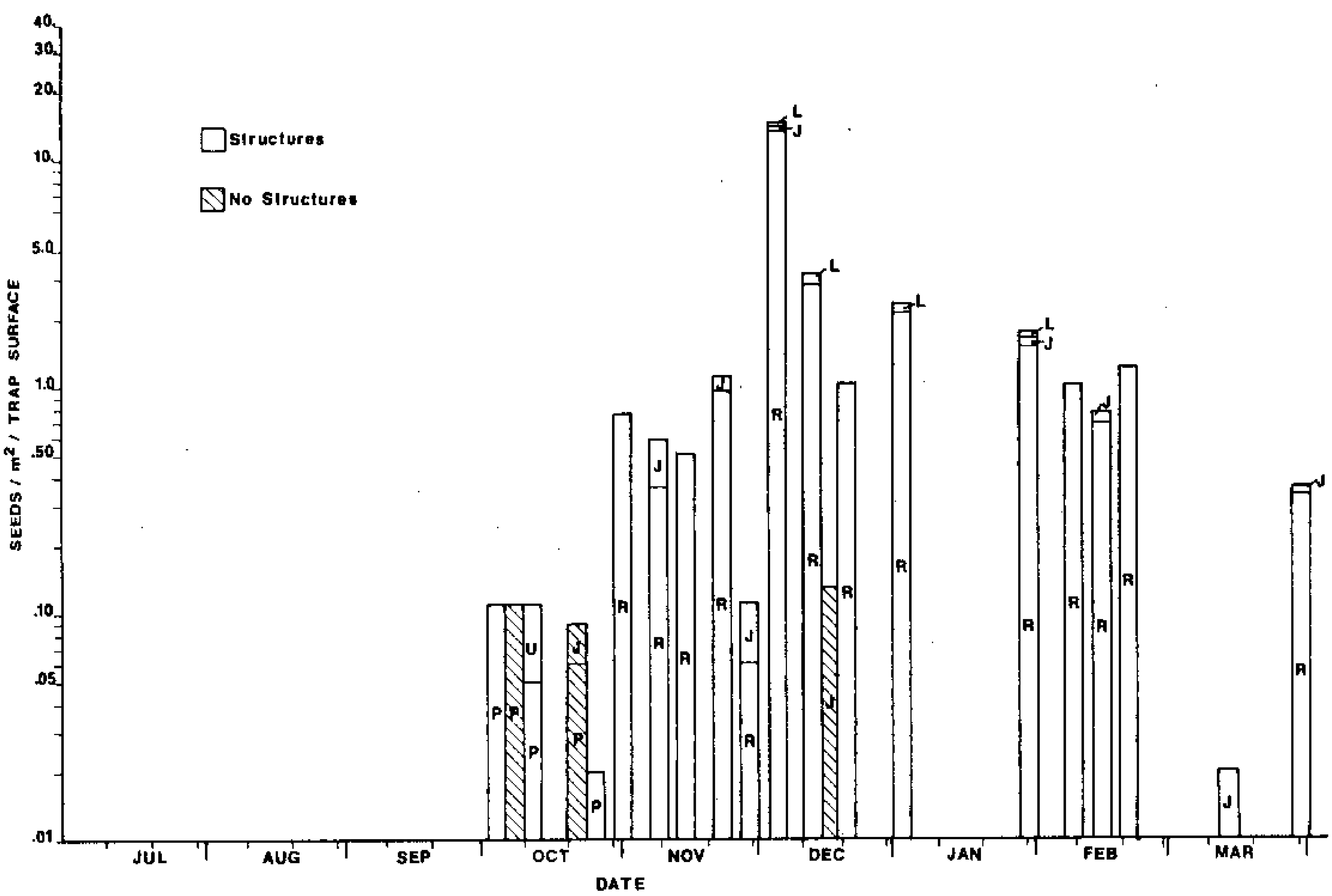

Fig. 5. Input of bird-dispersed seeds into fields D-5 (with artificial structures) and D-6 (no structures) from September 1980 to March 1981. The vertical axis is a log scale. Key: *J*, *Juniperus virginiana*; *L*, *Lonicera japonica*; *P*, *Phytolacca americana*; *R*, *Rosa multiflora* and *U*, unknown

from the analysis. In the complex field *J. virginiana* was the only species which had higher abundance in the field than on the edge or in the forest. Higher rates of non-*Juniperus* seed deposition were found in traps closer to the forest edge (Fig. 3). Even without *J. virginiana* seed input, there is a significant difference in total seed input into the two fields ($P<0.05$, Table 3).

Timing of seed deposition in the traps was influenced by fruit ripening times and relative nutritional value of the fruit (Baird 1980; Stiles 1980), as well as the movements of flocks of frugivorous birds. For the complex field peak seed deposition of *P. serotina* occurred in early September, of *C. florida* in late October and of *J. virginiana* in late October and again in mid-November. *R. multiflora* and *Toxicodendron radicans* (L.) Kuntze were deposited in early December and on into the next year (Fig. 4).

Artificial Structural Complexity

Over a period of 28 weeks from September 13, 1980 through March 31, 1981 a total of 1062 seeds from 87 droppings were recovered from fields D-5 (structures) and D-6 (no structures), henceforth referred to as the artificially complex field and simple field D-6 respectively.

One species, *Rosa multiflora*, accounted for 93% of the total seed input, followed by *Juniperus virginiana* (3.2%), *Lonicera japonica* Thunb. (2.4%) and *Phytolacca americana* L. (1.6%) (Table 4). Approximately 90% of the seed input into the fields occurred after November 20 (Fig. 5).

Table 5. Analysis of variance table for total seed input into Field D-5 using square root transformed data. Rows and columns refer to latin square design

Source of variation	df	SS	MS	F value
Total	35	516.1	14.7	
Rows	5	171.5	34.3	
Columns	5	39.9	7.9	
Treatment (structure)	5	116.0	23.2	2.45 NS
Error	20	188.62	9.4	

NS = No significant difference

During September and early October the seed input into both fields was low. A total of 18 seeds was found, the most common being *P. americana*. After the second week of October very few seeds were found in the simple field, while seed input into the artificially complex field increased dramatically (Fig. 5). This was due to the increased input of *R. multiflora*, *J. virginiana* and *L. japonica*. All total, 11 seeds (4 *J. virginiana* and 7 *P. americana*) in 5 droppings were found in the simple field D-6. This represents 1.1 seeds/m^2 of trap surface. In contrast, a total of 1051 seeds from 82 droppings was found in the artificially complex field (29 seeds/m^2/trap surface). There was a significant difference in seed input to the two fields (Mann-Whitney test, $P<0.01$).

The structure with the greatest number of seeds was the real plant (*Acer rubrum*), followed by horizontal, pyramid, arched, vertical and no structure (Table 4). A square root transformation was done to stabilize the variance (Snedecor and Cochran 1974). Analysis of variance indicates there is no statistically significant difference in the seed input into the different structural types or traps without structures (Table 5).

In summary, there was a significantly greater number of seeds input into the artificially complex field than simple field D-6. In the artificially complex field there was no statistically significant difference in seed input into the different structural types or the traps without structures.

Discussion

The pattern of seed deposition by birds in old fields is influenced by the vegetation structure and the availability of fruits. We have tried to separate these effects by examining the patterns of seed deposition by birds (1.) at the forest, (2.) in fields next to a forest edge, one with complex vegetation structure including fruiting individuals and the other with simple vegetation structure, (3.) in a field with artificial structures separated from the forest edge, and (4.) in a field without either natural or artificial structures and separated from the forest.

Natural Structural Complexity: Forest Edge and Succession

The numbers of seeds deposited in traps at the forest edge were far greater than in any of the field traps (Fig. 3). The trees at the forest edge provide perch sites for birds, whereas no other traps in these fields had overhanging perches. Also, the forest is a source of fruits eaten by the birds.

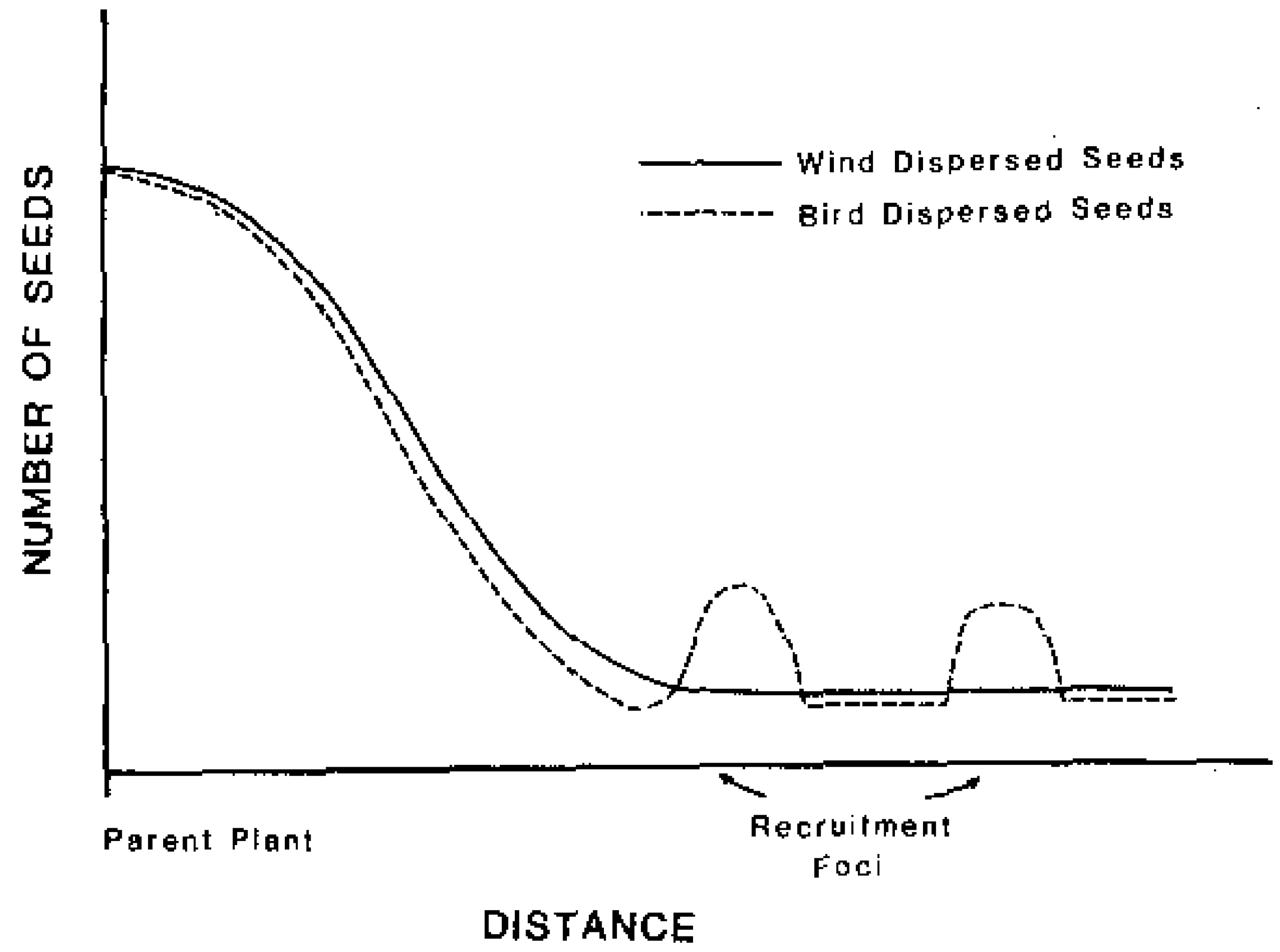

Fig. 6. A diagrammatic representation of the dispersal pattern of wind and bird-dispersed seeds

Seed deposition rates in complex field Z-4, a 13 year old field dominated by *J. virginiana* and *C. florida*, were influenced by the vegetation composition and structure of the field. The movement of birds from the edge to the field and vice-versa can be illustrated by the relationship between *J. virginiana* and *Vitis* spp. No *J. virginiana* grew at the edge and no *Vitis* spp. grew in the field, yet seeds of *Vitis* spp. were carried well into the field (3.8 seeds/m^2/trap surface) and *J. virginiana* was carried to the edge (45 seeds/m^2/trap surface). This movement of birds causes increased rates of deposition over that found in simple field D-8.

The majority of seeds deposited in the traps in complex field Z-4 was of species that were fruiting within the field. All species with the exception of *P. serotina* and *Vitis* spp. had at least one fruiting individual within the field. Only *J. virginiana* and *R. multiflora* were represented by a fruiting individual within 10 meters of a trap with the exception of the edge trap. The edge trap was located beneath the canopy of a *Prunus serotina*. The extent to which the presence of fruit influenced increased seed deposition and the extent to which the rate is a function of the structures available in the field will be examined below.

The lower seed deposition rates in simple field D-8 were a function both of low fruit availability and low structural complexity of the field. Bird movement into simple field D-8 from the forest edge was not increased by the presence of fruit in the fields or perches. Seed deposition at the edge was also lower than for complex field Z-4. We have observed *Turdus migratorius* and *Bombycilla cedrorum* flying from the edge into complex field Z-4 to feed, and back to the edge. The edge apparently provides more protective cover. Both the attraction of birds to the edge to feed on fruits in the field, and returns by birds to the edge for more protection increase the number of seeds deposited at the edge.

Artificial Structural Complexity

Field D-6, the simple field, followed the expected pattern of seed deposition with very few seeds being deposited in the traps (Fig. 5). Deposition rates were lower than those in simple field D-8 (1.1 seeds/m^2/trap surface for D-6 versus 7.4 seeds/m^2/trap surface for D-8). The greater distance from the forest edge to traps in simple field D-6 may have contributed to this result.

The seed deposition rate for artificially complex field D-5 was more similar to that for the field traps in complex field Z-4 than simple field D-6 or D-8 (29 seeds/m^2/trap surface for D-5 versus 53.2 seeds/m^2/trap surface for Z-4). The lower deposition rate in artificially complex field D-5 may be a result of increased distance from the edge (Fig. 3), the lack of fruit and the lower densities of structures in the field. Fruit acts both as an attractant for birds and a primary seed source. In complex field Z-4 when *J. virginiana* seeds are not included, there is a higher rate of seed deposition in the traps 15 m from the forest edge (Fig. 3). The abundance of seeds at this location illustrates movements of birds perpendicular to the forest edge, not found in simple field D-8.

Species diversity of seed input into the fields was also different. Complex field Z-4 and simple field D-8, had a greater diversity of seeds than artificially complex field D-5 and simple field D-6. This appears to be a function of both availability of fruits and time of year seeds were collected. Structurally complex field Z-4 and simple field D-8 were adjacent to the forest edge and thus closer to available fruits. They also were sampled one month earlier than either artificially complex field D-5 and simple field D-6.

The input of seeds into the artificially complex field was an order of magnitude greater than the input into simple field D-6. The herbaceous vegetation in both fields is very similar and both were equally distant from available seed sources. These data indicate that there is an increase of bird-disseminated seeds into fields that have some structural complexity, e.g. mimicking fields with a variety of vegetation types of different heights. The vegetation that protrudes above the single layer of herbaceous plants in the field functions as recruitment foci for bird-dispersed seeds.

When the input of seeds into traps under the different structural types and traps with no structures in the artificially complex field were compared, no statistical difference was found between them. Thus, it appears that the type of structure does not determine how effective the structure is as a recruitment focus. It is possible, however, that other factors such as height of the structure are more important. Additional studies are being conducted to determine at what height a structure becomes an effective recruitment focus for bird-disseminated seeds.

It is also interesting to note that the seed traps without structures in artificially complex field D-5 had significantly greater seed input than the traps in simple field D-6. It appears that the presence of structures in a field also increases the seed input into the surrounding area not directly under a structure.

The differences between artificially complex field D-5 and simple field D-6 illustrate the influence of perch sites, or vertical structure, on the pattern of seed input (Fig. 5). The pattern within artificially complex D-5 exhibited high seed input on the side of the field closest to the forest edge and a secondary peak on the side closest to a hedgerow, with much lower deposition rates in the center of the field (Fig. 3). Where specific food attractants are not involved it can be hypothesised that birds more often use the first perches encountered in an open field.

The temporal pattern of seed deposition into the fields is influenced by fruit availability, bird availability and the patterns of fruit choice by birds (Stiles 1980). The pattern from complex field Z-4 is illustrative: *Rubus* sp. ripens first, in July, followed by *P. serotina* ripening in August. *L. japonica*, an introduced species, does not ripen until October and *R. multiflora*, also introduced, does not ripen until November. The remaining species ripen by the end of the first week in September. Peaks of dispersal (Fig. 4) are associated with flocks of *Turdus migratorius* and/or *Bombycilla cedrorum* which visited the fields in October and November 1977.

Succession

In eastern North America, seed deposition in old fields by birds during secondary succession is at first low. Establishment of woody species such as *J. virginiana, C. florida, Fraxinus americana* L. and *Acer rubrum* provide perches for birds. This increases the rate of bird-disseminated seed input into a field by providing recruitment foci. Our data indicate that the presence of recruitment foci can increase seed input by more than an order of magnitude around the focus. Many of the invading woody species are bird dispersed, and as they reach reproductive age they become primary sources of propagules as well as foci for birds carrying other seeds. This suggests that the dispersal pattern of bird-disseminated seeds does not follow a smooth decay curve, but instead is characterized by distinct peaks (Fig. 6). These peaks represent the increased number of seeds which occur under the recruitment foci.

Heterogeneous seed shadows such as this have been reported for frugivorous bats (Fleming and Heithaus 1981, Janzen et al. 1976). In both cases, large concentrations of seeds were found at roosting sites, some up to 100 m from the parent tree. Studies of tropical frugivorous birds have also documented large concentrations of seeds under fruiting trees (Howe and Primack 1975, Howe 1977). Little or no quantitative data is available on the concentration of seeds under non-fruiting recruitment foci.

Gyphis et al. (1981) found significantly more of the bird-disseminated shrub, *Acacia cyclops* A. Cunn. ex G. Don., occurring under tall indigenous shrubs than in surrounding, sparser and shorter vegetation on Cape Peninsula, South Africa. Similarly, Gleadow and Ashton (1981) found bird-dispersed *Pittosporum undulatum* Vent. aggregated under existing bushes and trees in eucalypt forests of Central Victoria, Australia as were *Cotoneaster pannosa* Frach. and *Ilex aquifolium* L.

Hooper and Bullington (1972), studying previously cultivated land in Ogle County, Illinois that had been left fallow and uncut for six growing seasons, found high concentrations of bird-dispersed plants growing under powerline poles. They concluded that the introduction of these man-made structures has increased the rate of woody plant species invasion into the area.

Recruitment foci serve as the center of establishment and subsequent growth of bird-dispersed species into an area. These eventually form patches or clumps of vegetation which are unique in both structure and composition from the surrounding matrix of vegetation. The effect these patches have on the spatial dynamics of succession has previously been discussed by Yarranton and Morrison (1974) in their "nucleation" theory.

In conclusion, frugivorous birds may influence vegetation patterns, but existing vegetation, particularly the presence of recruitment foci, may also influence recruitment of new individuals by affecting bird movement and subsequent seed dispersal patterns.

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