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Selective Predation on the Seeds of Woody Plants

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Selective predation on the seeds of woody plants[1]

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MEINERS, S. J. AND E. W. STILES (Department of Ecology, Evolution and Natural Resources, Rutgers University, P.O. Box 231, New Brunswick, NJ 08903-0231). Selective predation on the seeds of woody plants. J. Torrey Bot. Soc. 124: 67–70). 1997.—Seed predation may be an important factor influencing the structure of successional plant communities. We used a cafeteria-style experiment, placed in an old field and an early successional forest, to determine predator preferences for seeds of nine species of woody plants. Intensity of seed predation was equivalent in both sites. Seed predators preferred *Acer saccharum, Ilex verticillata,* and *Viburnum dentatum,* but this was not related to seed mass. Predation intensity was more variable in the old field than in the forest, possibly related to the higher ground-layer heterogeneity of the old field site. We conclude that predator choice will allow some species to escape seed predation, potentially altering future plant community composition.

Key words: Feeding preference, Seed predation, Succession, Tree seeds

The establishment of woody plants in successional habitats is regulated by many limiting factors, which interact to produce the new plant community. Once limitations of site availability and seed dispersal are overcome, factors affecting individual species' performance regulate final community composition (Pickett et al. 1987). Seed predation is an important process which limits the establishment of trees in successional habitats (De Steven 1991; Gill and Marks 1991; Whelan et al. 1991; Myster 1993; Myster and Pickett 1993; McCarthy 1994; Hammond 1995). If seed predators exhibit preferences for individual species, successional rates and/or directions may be altered (Davidson 1993). Seed predators often show selective predation on a subset of the species available within a community. This selectivity may be based on characteristics such as seed size (energy content), nutritional content, handling time, and local abundance (Kaufman and Collier 1981; Price 1983; Kelrick et al. 1986). The result of such selective predation is a change in the relative species abundances of seeds which survive to germinate and establish. Selective predation may in this way alter the species composition of the plant community (Davidson et al. 1984).

The purpose of this study was to experimentally address the following questions: (1) Do predation rates differ among the seeds of co-occurring woody species?; and (2) are seed predators selecting seeds based on seed size/hardness?

Materials and Methods. Seeds of 9 woody species (trees, shrubs, and a vine) were collected in late September to early October 1994. All species were collected in the vicinity of Rutgers University, Piscataway, New Jersey USA except for *Viburnum dentatum,* which was collected near Trenton, New Jersey. The species selected represent locally common fall-fruiting woody species with a range of seed size and seed hardness. The species used were: *Acer negundo* L., *Acer saccharum* Marshall., *Fraxinus americana* L., *Ilex verticillata* (L.) A. Gray., *Juniperus virginiana* L., *Viburnum acerifolium* L., *Viburnum dentatum* L., *Viburnum prunifolium* L. and *Vitis vulpina* L. Fruit pulp was removed from the six bird-dispersed species (*Viburnum* spp., *Juniperus virginiana, Vitis vulpina,* and *Ilex verticillata*) to distinguish seed predation from fruit consumption by dispersers. Subsamples of 25 seeds were selected to determine the mean fresh seed mass of each species. The papery pericarp was removed from the *Acer* and *Fraxinus* species for mass determinations (Table 1). Of the 6 bird-dispersed species used in this study, *Vitis vulpina* has the thickest seed coat and *Juniperus virginiana* and *Ilex verticillata* the thinnest, with the *Viburnum* species intermediate in thickness. The wind-dispersed species had the thinnest seed coat of the species used with only a papery pericarp protecting the seed (USDA 1948).

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A single 5 m × 10 m plot was established on 10 October 1994 in an old field (8 years old) and in an adjacent early successional forest in the Hutcheson Memorial Forest (HMF) near East Millstone, New Jersey (40° 30′ N, 74° 34′ W). The old field site was bordered on three sides by forest and contained a few scattered trees and shrubs, including reproductive individuals of *Juniperus virginiana, Viburnum prunifolium,* and *Rosa multiflora*. Herbaceous cover was dominated by several species of *Solidago* with *Aster* spp., *Achillea millefolium, Daucus carota,* and *Bromus tectorum*. The canopy of the forest site was dominated by *Acer rubrum* and *Quercus palustris* with senescent *Juniperus virginiana* present. The understory of the site was very sparse, containing a few small *Viburnum prunifolium* and *Rosa multiflora* shrubs with little herbaceous cover. All species used within this study can be found in HMF (Frei and Fairbrothers 1963) within 200 m of the study sites. *Quercus palustris* acorn production was very low in 1994 and was not included in this study. *Acer rubrum,* the co-dominant of the stand, was not included because it reproduces in the spring.

Within each plot, 50 seed stations were placed regularly at 1 m intervals to provide an unbiased sample of the vegetation within the plot. Each station consisted of a 9 cm petri dish containing a single seed of each species (9 seeds total). The open nature of the dishes allowed all potential seed predators (mammals, birds, and invertebrates) access to the dish. Seed predators common to the site were white-footed mice (*Peromyscus leucopus*), gray squirrels (*Sciurus carolinensis*), slugs (*Deroceras reticulatum* and others) and seed-eating birds such as white-throated sparrows (*Zonotrichia albicollis*), song sparrows (*Melospiza melodia*), and house finches (*Carpodacus mexicanus*). Each 3–4 d the seed stations were censused and any missing seeds replaced to consistently provide predators with all species to chose from. This was continued for 42 d (until 21 November). Any seed which was missing from the dish and not on the adjacent soil (within 30 cm) was considered removed by a predator. Any dish which had been disturbed by white-tailed deer (*Odocoileus virginianus*) was replaced and excluded from the analysis for that period. The data from one census (day 14, October 24) were excluded because a heavy rain washed many seeds out of the dishes, making detection of predator removal impossible.

Seed preference was determined by ranking seed removal of each species within each dish, with ties assigned mean rank values. Ranks ranged from 1 to 9, with 1 being the least preferred. Dishes receiving little predation ($\leq$3 seeds removed) were removed from the preference analysis. The ranked data for each site were analyzed by Friedman's non-parametric two-way ANOVA followed by pair-wise comparisons (Marascuilo and McSweeney 1977). Mean number of seeds removed for each species was also calculated for each site.

Results. Overall 371 seeds were removed from the field plot and 375 from the forest plot. While the mean number of seeds removed per dish in both sites was very close (7.42 field, 7.50 forest), the variance of seed removal among dishes was significantly greater in the field site ($s^2 = 32.17$ field, $s^2 = 13.15$ forest; $F = 2.45$, $P < 0.01$). The distributions of total seed removal show the forest site to have an approximately normal distribution (Proc UNIVARIATE, SAS Institute Inc.; $P = 0.4898$) and the field to have a non-normal, bi-modal distribution ($P = 0.0009$) with few dishes having intermediate levels of seed removal.

Seed predators did show significant preference for some species, differing only slightly between sites (Table 1). *Ilex verticillata* and *Acer saccharum* (mean rank 5.54–6.42) were always highly preferred, while *Acer negundo* and *Fraxinus americana* were never preferred (mean rank 2.87–4.41). Three species changed in preference between sites; *Juniperus virginiana, Vitis vulpina,* and *Viburnum dentatum*. *Viburnum dentatum* switched from highly preferred in the field site (rank 9) to low preference in the forest site (rank 3). The other two species also declined in preference from the field to forest site, but the change was less extreme. Spearman's rank correlations of seed mass to mean preference also show no significant relationship in either the field ($r_s = 0.0833$, $P = 0.831$) or forest ($r_s = 0.0333$, $P = 0.932$) sites.

Discussion. There were significant differences in predation preference among species in this study. This selectivity does not appear to be correlated with any obvious morphological characters of the seeds. Wind-dispersed species, with papery seed coats, were not consistently preferred over the harder bird-dispersed species as would be predicted based on handing times (Kaufman and Collier 1981). Seed preference was also not significantly related to seed size in either habitat over the range of seed masses

Table 1. Mean preference measurements and mass (n = 25) for the seeds of nine woody species used in the predation experiment. Mean number of seeds removed and preferences are given for each species in the field (n = 35) and forest (n = 43). Preferences range from 1 to 9 with 1 being the least preferred. Mean preferences within a column with the same letter are not significantly different ($P > 0.05$). For ease of comparison, preference rank within each site is provided.

		Seed removal		Preference			
Species	Seed mass (mg)	Field	Forest	Field	Rank	Forest	Rank
Acer saccharum	58.5	1.34	1.64	5.77^{a}	8	6.42^{a}	9
Ilex verticillata	4.4	1.37	1.31	5.54^{a}	7	6.08^{a}	8
Juniperus virginiana	9.9	1.26	1.29	5.19^{ab}	4	5.95^{ab}	7
Viburnum acerifolium	45.6	1.23	1.14	5.31^{ab}	6	5.29^{abc}	6
Vitis vulpina	50.8	0.89	1.12	4.56^{ab}	3	5.59^{abc}	5
Viburnum prunifolium	124.0	1.23	0.79	5.26^{ab}	5	4.67^{abc}	4
Viburnum dentatum	38.3	1.43	0.43	6.01^{a}	9	3.69^{bc}	3
Acer negundo	39.1	0.86	0.40	4.41^{ab}	2	3.65^{bc}	2
Fraxinus americana	21.3	0.31	0.40	2.87^{b}	1	3.54^{c}	1

tested. This may be the result of selection by the predators on some other seed character such as nutrient content (Price 1983; Kelrick et al. 1986). Alternatively, the lack of preference based on seed size could be due to predation by the entire guild of seed predators. Individual predator species may have been selecting seeds within a small size range (Price 1983). Because of the diversity of body sizes in the seed predator guild, the whole range of seed sizes were removed.

The spatial patchiness within habitats described in other studies was also observed in the field habitat of this study. Some dishes had consistently high removal rates while others had little or no seed removal. Patchiness of the field habitat may be related to the home ranges of mammalian seed predators (Webb and Willson 1985) or to the heterogeneity of the vegetation structure of that site (Whelan et al. 1991). Within the field site, there were patches dominated by tall herbaceous cover (i.e., *Solidago* spp.), low herbaceous cover, and sparse woody cover (*Rosa multiflora* and *J. virginiana*). This ground-layer heterogeneity of habitat structure was lacking in the forest site, which was a continuous matrix of tree trunks, leaf litter and small branches. Interestingly, this site also lacked spatial variation in seed removal.

By selectively feeding on seeds of woody plants, predators have the potential to alter successional dynamics within a site (Pickett et al. 1987; Davidson 1993), altering future community composition. Selective predation may cause the abundance of species with non-preferred seeds to be higher than would be expected based on competitive abilities or physiological traits. In habitats with high variation in seed predation intensity, sufficient safe sites may exist to allow the establishment of preferred species. The preferences found in this study, do not clearly relate to seed size or hardness, preventing prediction of preferences for other species. Small-scale differences in vegetation structure may affect the spatial pattern of seed predation, and should be the focus of future studies.

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