OIKOS 58: 55–60. Copenhagen 1990

Microdisturbances in oldfields and forests: implications for woody seedling establishment

Brian C. McCarthy and José M. Facelli

McCarthy, B. C. and Facelli, J. M. 1990. Microdisturbances in oldfields and forests: implications for woody seedling establishment. – Oikos 58: 55–60.

We investigated the range and extent to which different microdisturbances could have an impact on woody seedling establishment in seral oldfields and mature forest on the New Jersey Piedmont, USA. We measured the frequency of small-scale disturbances by following the fate of artificial, plastic structures, designed to hold a point space the approximate size and shape of a one-yr-old tree seedling. We placed the models in three habitats of contrasting age and structure: two oldfields (4 and 18 yr old) and an oldgrowth forest (> 300 yr old). We followed the fates of the models for 275 d, and assessed both the proportion of models damaged at each site and the cause of disturbance. After ten months, the disturbance rate was ca. 25% in both fields and 55% in the forest. Causes of microdisturbances were different in each habitat. Models in the youngest field were damaged primarily by snow and frost heaving during winter; gnawing by vertebrates was the predominant disturbance in the older field; trampling accounted for the greatest percentage of damage in the forest. Herb cover and proximity to a shrub, tree, or fallen log also affected disturbance rate. This study demonstrates the potential importance of the microdisturbance regime on woody seedling establishment in oldfields and forests, and the relevance of temporal and spatial complexity on the determination of that regime.

B. C. McCarthy and J. M. Facelli, Dept. of Biol. Sci., Rutgers Univ., P.O. Box 1059, Piscataway, NJ 08855, USA (present address of BCM: Dept of Biology, Frostburg State Univ., Frostburg, MD 21532, USA).

Introduction

Many different disturbances affect community structure and dynamics (White 1979, Pickett and White 1985) at various hierarchical levels and spatial scales (Pickett et al. 1989). Disturbances include the effects of herbivory, frost heaving, snow and ice, windstorms, landslides, drought, flooding, and fire (reviewed in White 1979 and Pickett and White 1985). Some of these factors act at relatively large spatial scales, and extensively alter community structure and heterogeneity. Moreover, these large scale disturbances are generally insensitive to the structural heterogeneity of the community. Other disturbance agents act at much smaller scales, and their impact may be affected by the present community heterogeneity. Examples are the fall of tree limbs (Abell 1934, Lemon 1961, Johnson 1987), burrowing (Platt 1975, Goldberg and Gross 1988), and trampling by animals (McNaughton 1983). These disturbances, though not extensive, may significantly alter habitat heterogeneity and, at certain frequencies and intensities, could affect community dynamics.

Ample attention has been devoted to disturbances produced by animals (reviewed by Harper 1977, Crawley 1983, Denno and McClure 1983, Strong et al. 1984). However, the majority of studies tend to focus on their primary effects; i.e., grazing (McNaughton 1979), browsing (Adams 1975), parasitism (Warrington and Whittaker 1985), etc. Other consequences of animal activities, or secondary effects (McCormick and Andresen 1960, Spedding 1971, Harper 1977), such as trampling, wallowing, etc., have not received equal attention, nor have they been regularly evaluated with field experiments. While there is a plethora of information

Accepted 26 January 1990

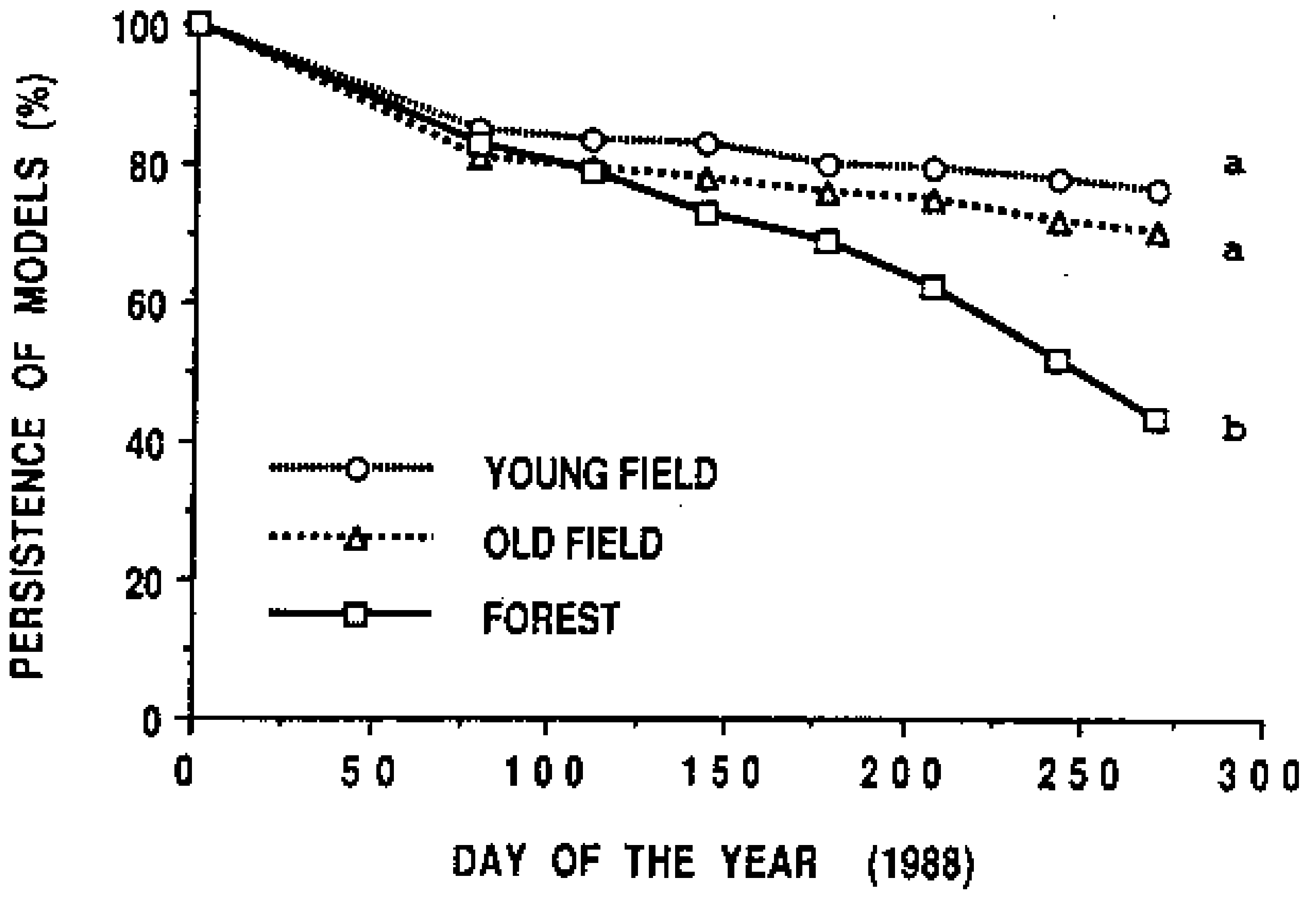

Fig. 1. Persistence (percentage remaining undisturbed) of the plastic models in a 4-yr oldfield ("young field"), an 18-yr oldfield ("old field"), and a 300-yr oldgrowth mixed-oak forest on the New Jersey Piedmont. Habitats having a similar ($P > 0.05$) number of models surviving to day 275 are indicated by the same letter.

on the influences of disturbances by grazing livestock (e.g., Quinn and Hervey 1970, Spedding 1971, Coffin and Lauenroth 1988) and native mammals (Platt 1975, McNaughton 1983, Collins and Barber 1986) in grasslands, there is little information on the secondary effects of mammals in oldfields and forests (but see Adams 1975, Tilman 1983, Goldberg and Gross 1988). Secondary effects may result in a mosaic superimposed upon the heterogeneities already created through grazing (Harper 1977, McNaughton 1983, but see Facelli et al. 1989). Litterfall is another example of a small-scale disturbance that has been infrequently evaluated (but see Harcombe and Marks 1983, Clark and Clark 1989).

There is a growing body of evidence to suggest that biotic and abiotic disturbances may have the greatest effects early in the life-history of a plant, because seeds and seedlings of most plants are particularly sensitive to both biological enemies and physical damage (Grubb 1977, Cook 1979, Clark and Clark 1989). Abiotic and secondary animal effects on tree seedlings are difficult to separate from direct biotic effects in standard field experiments, but are amenable to experimental evaluation through the use of simple artificial plastic structures (Clark and Clark 1989). Artificial models are sensitive to small-scale disturbances that can physically damage tree seedlings, but are free of the species-specific and density-dependent effects associated with live plants (Clark and Clark 1989).

Here we report an evaluation of the frequency of abiotic and secondary biotic microdisturbances that can kill or damage woody seedlings, using an artificial seedling assay technique. We address two questions: (1) What is the frequency of different microdisturbances that can potentially affect woody seedling establishment in different oldfield and forest habitats? (2) How does macro- and microhabitat influence the frequency of occurrence of those microdisturbances?

Methods

Study site

Our study was carried out at the William L. Hutcheson Memorial Forest Center (HMF) in East Millstone, New Jersey, USA (43° 30'N, 74° 34'W). The climate is subcontinental, receiving approximately 112 cm of precipitation distributed throughout the year (Biel 1958). The mean annual temperature is 11.7°C, with the mean monthly temperature ranging from 0.0°C in January to 24° C in July (United States Weather Bureau 1959). The forest and fields of the study are located on well drained silty-loam soils derived from the Triassic red shales of the Brunswick Formation (Wolfe 1977).

HMF comprises a 26 ha forest patch, and a surrounding matrix of agricultural fields, oldfields, and woodlots. The vegetation of the forest and the oldfields is well documented (Bard 1952, Buell 1957, Frei and Fairbrothers 1963, Pickett 1982). The dominant overstory trees of the forest are *Quercus alba, Q. rubra, Q. velutina, Carya ovalis*, and *C. ovata. Cornus florida* and *Viburnum acerifolium* are the principal understory species. Braun (1950) includes this area in her oak-chestnut region. While the forest is uncut, there is much evidence of natural disturbance including fire in the 1600s, hurricanes in the 1950s, drought in the 1950s and 1960s, and gypsy moth caterpillar infestations; most of these factors continue to have an impact upon the forest. Repeated gypsy moth outbreaks in recent years, combined with the weakened tree limbs associated with trees of great age (200+ yr), have resulted in the death of many large limbs and whole trees which lie upon the forest floor.

We studied one site selected in the forest, and two sites in adjacent oldfields; all three sites were within 200 m from each other. The younger field was abandoned from agriculture in 1983. The vegetation of this field is dominated by a mixture of perennial herbs such as *Solidago* spp., *Aster* spp, *Daucus carota*, and *Hieracium florentinum*. Scattered young shrubs of *Rosa multiflora* are also found. The older field was abandoned from agriculture in 1966. The structure of the vegetation in this field is savanna-like with a diverse mixture of understory perennial herbs and scattered woody plants. The dominant tree is *Juniperus virginiana*. This field also has a high coverage of woody vines and thorny shrubs including *Lonicera japonica, Toxicodendron radicans, Rosa multiflora,* and *Rubus flagellaris*.

Experimental methods

The ideal experimental unit to examine the secondary effects of large mammals and the influence of abiotic forces at the microsite level should meet two criteria. The unit must be unresponsive to direct biotic influences (i.e., have neutral palatability, be insensitive to pathogens, etc.) as well as unresponsive to ordinary environmental conditions. It is also desirable that the

Tab. 1. Percentage of artificial seedlings which suffered various forms of disturbance and which survived ten months without being disturbed in three habitats on the New Jersey Piedmont. Percentages are based on 200 seedlings per habitat.

Fate after 10 months	Young field (4-yr old)	Old field (18-yr old)	Forest (300-yr old)
Disturbed by:			
Frost heaving	9	4	2
Litterfall	2	2	2
Trampling	3	3	22
Vertebrates	4	14	17
Unknown	5	6	13
Undisturbed	77	71	44

unit should be constructed so as to emulate in size and shape a real tree seedling as much as possible. To meet these criteria we adapted an assay technique developed by Clark and Clark (1989). The assay technique utilizes a plastic structure of the approximate dimensions of a young tree seedling, constructed from two plastic drinking straws stapled in the form of a cross (see Fig. 1 in Clark and Clark 1989). Two wooden coffee stirrers were inserted into the vertical base, and stapled, with 10 cm left protruding to act as a rudimentary "root". The top of the cross was doubled over and stapled to prevent water and ice accumulation. The straws were white in color, 20 cm in length, and 0.6 cm in diameter. The color of the straws apparently has little influence on vertebrate recognition (D. Clark, pers. comm.).

In each of the three habitats (unreplicated) we placed 200 models in four parallel 50 m transects spaced 10 m apart, and marked at 10 m intervals with pink flagging. Models were "planted", to the full depth of their "root", every 1 m along the transect. A few exceptions were made to circumvent large tree boles; however, in all other cases we took great care to place the model at the designated sample points along the transect. Thus, models were placed into large thickets of thorny shrubs such as *Rosa multiflora* and *Rubus* spp., dense thickets of the vines *Lonicera japonica* and *Toxicodendron radicans*, and adjacent to dead logs. After the models were placed we categorized the microhabitat surrounding each of the 600 models. We defined the realm of microhabitat influence arbitrarily as the volumetric space around each model demarcated by a 0.5 m hemispherical diameter, centered at the base of the model. We recognized five microhabitat types, based on the dominant structural properties of the vegetation within the defined space: a) shrub or dense vines, b) tree, c) log, d) dense herb cover, e) sparse herb cover.

Beginning in January 1988, individuals were censused eight times over 275 d at intervals of 25–35 d. No data were collected between days 15–75 of that year due to snow cover. A microsite was defined as disturbed when either of the two arms of the model touched the ground, the model was completely flattened, or when it was ripped from its original position. Each damaged model was carefully evaluated to determine the source of the disturbance. We recognized five disturbance categories: frost heaving, litterfall, trampling, vertebrate gnawing, and unknown. A model was considered disturbed by "frost heaving" when it was found intact yet lying on the ground during the winter months. Repeated freezing and thawing of the ground would work some models to the surface. While the rudimentary "root" of the models was made to be somewhat similar to the tap root of a one-yr-old broad-leaved tree seedling, the lack of higher order branching on the models certainly produces an overestimate of disturbances due to frost heaving. However, this estimate is still of value as a "worst-case" scenario, and, perhaps more importantly, it allows for a cross comparison among habitats. Microdisturbances due to litterfall involved the model being crushed by a tree branch, or, as in the fields, a heavy buildup of dead perennial herbs or vines that brought down a model. We scored disturbance by trampling when hoof marks from white-tailed deer (*Odocoileus virginianus*) were clearly visible in the original position of a crushed model. Models were scored as "vertebrate damaged" when teeth or claw marks were found on the plastic straws. If the source of disturbance was ambiguous, or the model could not be relocated, we assigned it to the "cause unknown" category.

Results

After 10 months, the proportion of models damaged was 21% in the youngest field, 26% in the older field, and 55% in the forest (Fig. 1). While the two fields did not differ significantly (P = 0.100) from each other, the frequency of disturbances in both of the oldfields was lower than that of the forest (P << 0.001; Kolmogorov-Smirnov two-sample tests, Sokal and Rohlf 1981).

The source of microdisturbances differed significantly (P < 0.001, df = 8; RXC Test of Independence, Sokal and Rohlf 1981) among habitats (Tab. 1). Frost heaving

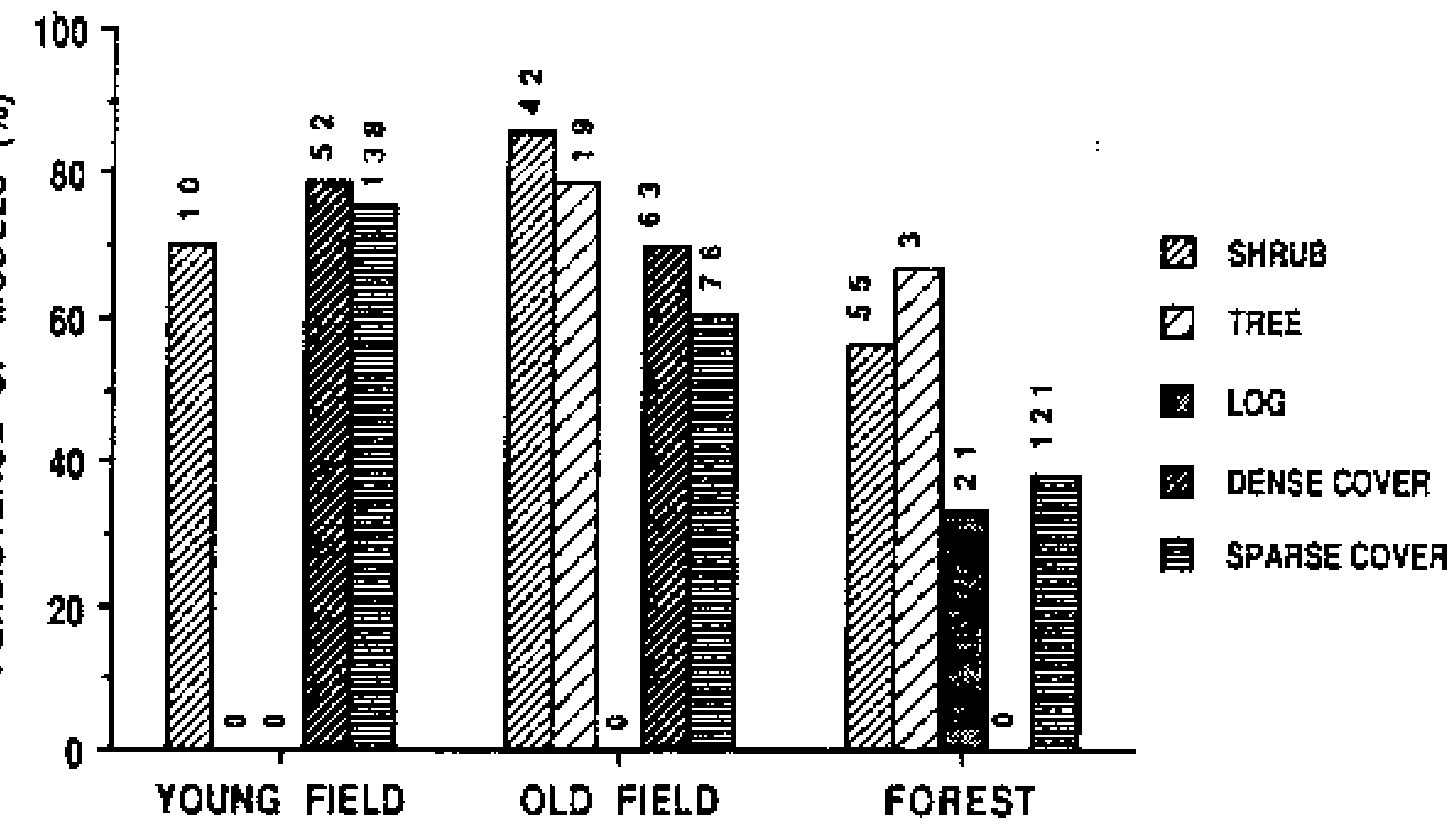

Fig. 2. Persistence (percentage remaining undisturbed) of artificial models in five contrasting microhabitats in two successional oldfields and in a mature forest (see caption Fig. 1) after 10 months. "Dense cover" and "sparse cover" refer to the relative abundance of herbaceous perennials. The number above each bar indicates the absolute number of models originally placed in that microhabitat (total of 200 per macrohabitat).

was more frequent in the young field. Possibly a good proportion of what we scored as "unknown" also belongs in this category. Models may have been heaved-up by frost during the winter but did not fall over, and therefore not scored as disturbed until spring. Most of the damage in the older field was due to vertebrates gnawing at the seedlings. Cottontail rabbits (*Sylvilagus floridanus*) seemed to be very active in this field and disturbed the models frequently. The most common microdisturbance in the forest was trampling by white-tailed deer, which are abundant in this forest. Temporal correlations were also evident; e.g., vertebrate damage was extremely low during winter months when snow protected seedlings from discovery.

Frequency of the different microdisturbances was significantly ($P < 0.001$; G-Test, Sokal and Rohlf 1981) influenced by microhabitat (Fig. 2). Due to the absence of trees in the youngest field there was not a great diversity of microhabitats and damage was similar among all the microhabitats available. Disturbance was lowest in the older field when a model was beneath dense (often thorny) shrub cover or a tree. In the forest, the greatest proportion of models disturbed were adjacent to a log or in the open (i.e., sparse ground cover).

Discussion

We have shown that microdisturbances due to abiotic forces and secondary animal effects may reach frequencies of 21–55% over a ten month period in the habitats we studied. We consider that, given those frequencies, microdisturbances may potentially affect the establishment of woody plants, and may constitute a factor strong enough to affect structural components at the community level. We also found that different sources of microdisturbances may be important among different habitats, and that the structural heterogeneity of the site may affect the frequency and distribution of different destructive events.

Frost heaving is an influential force arresting the invasion of plants in early seral habitats (Small et al. 1971, Buell et al. 1971, Watt 1981). This factor has not received enough study, though it is likely to be a contributing influence on woody plant establishment in temperate zone habitats. Newly abandoned fields are dominated by herbs that die back to the ground each year, affording little or no protection from snow, ice, and freezing rain. A buildup of litter and vegetation cover over a number of years may be needed to provide a sufficient safe site for woody seedling establishment (Pickett et al. 1987).

Damage attributable to falling litter was minimal (2–5%) in all three habitats we studied, contrasting with results from Clark and Clark (1989) who found that the proportion of seedling models destroyed by macro-litterfall after one year was nearly 20% in a tropical wet forest. Our results are closer to, though still lower than, those from Harcombe and Marks (1983) who determined that ca. 12% of the death of young trees in a Texas hardwood forest was due to breakage by other trees. Wet tropical habitats produce a greater rain of litter onto the forest floor due to the high densities of epiphytes and lianas present in the canopy. Likewise, litterfall disturbance in all three of our habitats was generally correlated with the winter months when there was a buildup of snow and ice on canopy plants. Surprisingly, litter appeared to be a slightly greater source of disturbance in the youngest field. Snow and wind tended to bring down large patches of standing dead herbaceous material, that combined with additional snow accumulation, was sufficient to bend a seedling model to the ground.

Vertebrates uprooted or gnawed a good portion of the seedlings providing an unplanned but useful index of the relative activity of mammals. While much of this vertebrate activity could be attributable to a novelty effect, it should be recognized that the artificial seedlings were extremely inconspicuous during much of the year (as is a natural seedling). The models were covered by snow a good part of the winter, by vegetation during the summer, and by leaf litter during the autumn. Only in the early spring before leaf-out were the seedling models particularly conspicuous; concomitantly this is when many of the artificial models were damaged by gnawing. Overall, the frequency of damage of the models corresponds to the vertebrate abundance patterns observed in the three habitats. Based on visual sightings and scat frequency, the older field had the most vertebrate activity; correspondingly, this habitat had the greatest seedling disturbance rate by vertebrates. In another study performed at HMF, Myster and McCarthy (1989) found that a large proportion of one-year-old *Carya tomentosa* seedlings were damaged or destroyed by browsing mammals. The survival of a *Carya* seedling was patch dependent; those planted away from the forest-field ecotone (towards the oldfield) were less frequently disturbed.

Our data highlight the complex relationships existing amongst environment, vegetation, and animals during succession. Young seral communities are markedly affected by environmental extremes. These communities are structurally more homogeneous and have no protective litter or plant cover during late winter months – this results in great environmental exposure to establishing seedlings. As the community becomes structurally more complex, a greater number of environmentally buffered microsites become available (Watt 1981). Hence the impact of the environment on newly established seedlings is expected to decrease while the direct and indirect effects of vertebrate herbivores (capable of differentially selecting patches and microsites) increases. In early successional communities, where structural complexity is generally lacking, certain microhabitats (e.g. dense vine and thorny shrub patches) may provide a refugium for tree seedlings and thus permit establishment (Jaksić and Fuentes 1980). The frequency of disturbance in our study correlates directly with the density and complexity of ground cover, which may influence the actions of mammals in that habitat. Clearly, succession must be evaluated in terms of a multi-factor model, including spatial heterogeneity and providing for manyfold interactions, before we are able to attain a greater resolution to predict vegetation dynamics.

Interestingly, species which are important later in the successional sequence at HMF often invade and are present in earlier communities (Buell et al. 1971). Why then, if long-lived tree seedlings are present in the first 5–10 years, do the primary arborescent species not become dominant until the sixtieth year (Bard 1952) after abandonment? There is little doubt that herbivores may deflect succession entirely (Crawley 1983: 303), or alternatively, may act as 'keystone predators' (sensu Paine 1966) to control community structure. In addition to the direct effects of grazers on woody seedlings, we have demonstrated that secondary consequences of mammal activities and abiotic microdisturbances may also markedly contribute to thwarting the invasion of woody plants in seral habitats.

Acknowledgements – We thank D.B. and D.A. Clark for providing us with a preprint of their artificial seedling assay. D.A. Clark, P.J. Morin and J.A. Quinn provided helpful comments on the manuscript. E. D'Angela graciously helped to build the models. BCM and JMF acknowledge HMF for Summer Research Grant support. JMF was supported by Consejo Nacional de Investigaciones Científicas, Argentina.

References

Abell, C.A. 1934. Influence of glaze storms upon the hardwood forests in the southern Appalachians. – J. Forestry 32: 35–37.

Adams, S.N. 1975. Sheep and cattle grazing in forests: a review. – J. Appl. Ecol. 12: 143–152.

Bard, G.E. 1952. Secondary succession on the Piedmont of New Jersey. – Ecol. Monogr. 22: 195–215.

Biel, E.R. 1958. The climate of New Jersey. – In: Fink, S.J. (ed.), Economy of New Jersey. Rutgers Univ. Press, New Brunswick, NJ, pp. 53–98.

Braun, E.L. 1950. Deciduous forests of eastern North America. – Hafner Press, New York.

Buell, M.F. 1957. The mature oak forest of Mettlar's Woods. – William L. Hutcheson Mem. For. Bull. 1: 16–19.

– , Buell H.F., Small, J.A. and Siccama, T.G. 1971. Invasion of trees in secondary succession on the New Jersey piedmont. – Bull. Torrey Bot. Club 98: 67–74.

Clark, D.B. and Clark, D.A. 1989. The role of physical damage in the seedling mortality regime of a neotropical rain forest. – Oikos 55: 225–230.

Coffin, D.P. and Lauenroth, W.K. 1988. The effects of disturbance size and frequency on a shortgrass plant community. – Ecology 69: 1609–1617.

Collins, S.L. and Barber, C. 1986. Effects of disturbance on diversity in mixedgrass prairie. – Vegetatio 64: 87–97.

Cook, R.E. 1979. Patterns of juvenile mortality and recruitment in plants. – In: Solbrig, O.T., Johnson, G.B. and Raven, P.H. (eds), Topics in plant population biology. Columbia Univ. Press, New York, pp. 207–231.

Crawley, M.J. 1983. Herbivory: the dynamics of animal-plant interactions. – Univ. of California Press, Berkeley.

Denno, R.F. and McClure, M.S. 1983. Variable plants and herbivores in natural and managed systems. – Academic Press, New York.

Facelli, J.M., León, R.J.C. and Deregibus, V.A. 1989. Community structure in grazed and ungrazed grassland sites in the flooding Pampa, Argentina. – Am. Midl. Nat. 121: 125–133.

Frei, K.R. and Fairbrothers, D.E. 1963. Floristic study of the William L. Hutcheson Memorial Forest. – Bull. Torrey Bot. Club 90: 338–355.

Goldberg, D.E. and Gross, K.L. 1988. Disturbance regimes of midsuccessional old fields. – Ecology 69: 1677–1688.

Grubb, P.J. 1977. The maintenance of species-richness in plant communities: the importance of the regeneration niche. – Biol. Rev. 52: 107–145.

Harcombe, P.A. and Marks, P.L. 1983. Five years of tree death in a *Fagus-Magnolia* forest, southeast Texas (USA). – Oecologia (Berl.) 57: 49–54.

Harper, J.L. 1977. Population biology of plants. – Academic Press, New York.

Jaksić, F.M. and Fuentes, E.R. 1980. Why are native herbs in the Chilean Matorral more abundant beneath bushes: microclimate or grazing? – J. Ecol. 68: 665–669.

Johnson, E.A. 1987. The relative importance of snow avalanche disturbance and thinning of canopy plant populations. – Ecology 68: 43–53.

Lemon, P.C. 1961. Forest ecology of ice storms. – Bull. Torrey Bot. Club 88: 21–29.

McCormick, J. and Andresen, J.W. 1960. Some effects of animals on the vegetation of the New Jersey Pine Barrens. – Bull. Torrey Bot. Club 87: 375–385.

McNaughton, S.J. 1979. Grassland-herbivore dynamics. – In: Sinclair, A.R.E. and Norton-Griffiths, M. (eds), Serengeti: dynamics of an ecosystem. Univ. of Chicago Press, Chicago, pp. 46–81.

– 1983. Serengeti grassland ecology: the role of composite environmental factors and contingency in community organization. – Ecol. Monogr. 53: 291–320.

Myster, R. and McCarthy, B.C. 1989. Effects of herbivory and competition on survival of *Carya tomentosa* (Juglandaceae) seedlings. – Oikos 56: 145–148.

Paine, R.T. 1966. Food web complexity and species diversity. – Am. Nat. 100: 65–75.

Pickett, S.T.A. 1982. Population patterns through twenty years of oldfield succession. – Vegetatio 49: 45–59.

– and White, P.S. 1985. The ecology of natural disturbance and patch dynamics. – Academic Press, New York.

– , Collins, S.L. and Armesto, J.J. 1987. Models, mechanisms and pathways of succession. – Bot. Rev. 53: 335–371.

– , Kolasa, J., Armesto, J.J. and Collins, S.L. 1989. The ecological concept of disturbance and its expression at various hierarchical levels. – Oikos 54: 129–136.

Platt, W.J. 1975. The colonization and formation of equilibrium plant species associations on badger disturbances in a tall-grass prairie. – Ecol. Monogr. 45: 285–305.

Quinn, J.A. and Hervey, D.F. 1970. Trampling losses and travel by cattle on sandhills range. – J. Range Manage. 23: 50–55.

Small, J.A., Buell, M.F., Buell, H.F. and Siccama, T.G. 1971. Old-field succession on the New Jersey Piedmont the first year. – William L. Hutcheson Mem. For. Bull. 2: 26–30.

Sokal, R.R. and Rohlf, F.J. 1981. Biometry: the principles and practice of statistics in biological research. – Freeman, San Francisco.

Spedding, C.R.W. 1971. Grassland ecology. – Clarendon Press, Oxford.

Strong, D.R., Lawton, J.H. and Southwood, R. 1984. Insects on plants: community patterns and mechanisms. – Harvard Univ. Press, Cambridge.

Tilman, D. 1983. Plant succession and gopher disturbance along an experimental gradient. – Oecologia (Berl.) 60: 285–292.

United States Weather Bureau 1959. Climate of the states. New Jersey. United States Department of Commerce. Government Printing Office, Washington, D.C.

Warrington, S. and Whittaker, J. B. 1985. An experimental field study of different levels of insect herbivory induced by *Formica rufa* predation on sycamore (*Acer pseudoplatanus*). II. Aphiodea. – J. Appl. Ecol. 22: 787–796.

Watt, A. S. 1981. A comparison of grazed and ungrazed Grassland A in East Anglian Breckland. – J. Ecol. 69: 499–536.

White, P. S. 1979. Pattern, process, and natural disturbance in vegetation. – Bot. Rev. 45: 229–299.

Wolfe, P. E. 1977. The geology and landscapes of New Jersey. – Crane Russak, New York.