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Effects of herbivory and competition on survival of Carya tomentosa (Juglandaceae) seedlings

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We tested the effects of predation, above-ground diffuse competition and below-ground diffuse competition on the survival and growth of *Carya tomentosa* (Juglandaceae) seedlings in a five year oldfield bordering a mature forest. We planted eighty seedlings under cages, in pots or with surrounding vegetation tied back (in all combinations) to realize the treatments. We found that seedlings unprotected from herbivores suffered great mortality (i.e., survival < 10%). Seedlings planted away from the forest edge suffered significantly less predation than those closer to the forest. Seedlings often resprouted after browsing. Because only a few seedlings survived outside the cages, we focused on the caged seedlings to examine competition effects on seedling growth and survival. No significant differences were found in leaf, stem, root, and total biomass of surviving seedlings under any of the competition treatments. Insect herbivores affected 15% of the seedlings by removing 10% of their leaf area during the first year. In the second year, 30% had 1–10% damage to leaf tissue. No seedlings died due to invertebrate herbivores. Browsing by mammalian herbivores appears to be the primary factor determining woody seedling establishment patterns in seral oldfields.

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Introduction

The mechanisms which regulate populations and determine community structure have been of central concern to ecologists for decades (Hairston et al. 1960, Menge and Sutherland 1976). Empirical studies have demonstrated that communities may be structured by predation (e.g., Lubchenco 1983, Morin 1983), competition (e.g., Korstian and Coile 1938, Sagar and Harper 1961, Fowler 1981) or a combination of these mechanisms (Harper 1969, Menge and Sutherland 1976). Current research suggests that single factors are usually inadequate and unlikely to fully explain community structure (Pickett et al. 1987).

Several studies have examined how multiple mechanisms might influence community organization. Predation has been found to hold densities of potentially competing species at a level so low that contact-mediated competition between certain dominant taxa can be reduced or even eliminated (Paine 1966, Harper 1969, Lubchenco 1978, Morin 1983). Alternatively, predation may not preclude the occurrence of competition at all but rather act to maintain it (Buss 1986).

In terrestrial plant communities, the direct effects of mammalian herbivores (i.e., driving certain plants to local extinction through species-specific browsing) have received considerable attention (e.g., Adams 1975, Mack and Thompson 1982, Crawley 1983, McNaugton 1983). However, the effects of herbivores may also be indirect; e.g., feeding which alters the relative competitive abilities of plants and creates competition-free microsites. Herbivores can have a marked effect on vegetational processes such as succession (Crawley 1983). In oldfield communities, herbivores may potentially in-

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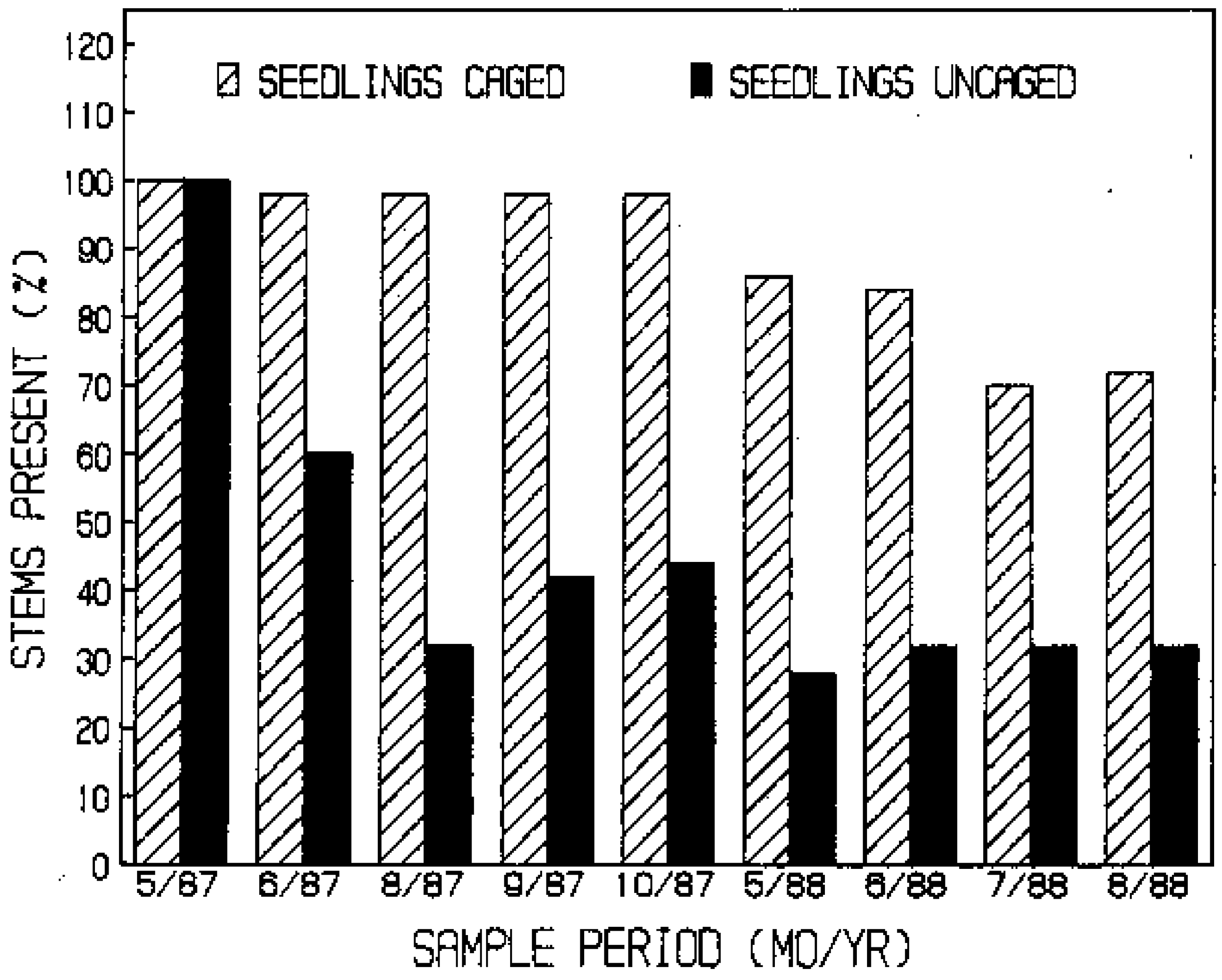

Fig. 1. Proportion of seedlings surviving when protected and exposed to browsing mammals. (K-S test, DN = 0.8888, P = 0.0016).

crease the rate of species replacement because of reduced competitive abilities of the resident plants (Watt 1971).

Removal experiments have suggested competition is an important structuring mechanism in oldfields (Pinder 1975, Raynal and Bazzaz 1975, Gross 1980, Hils and Vankat 1982). However, few studies have been conducted to specifically address the effects of competition and herbivory both individually and collectively.

Ecologists have frequently hypothesized on the factors that determine the rate of succession (Connell and Slatyer 1977). More specifically, why does it take trees so long to attain dominance in oldfields? Woody species are present early in oldfield succession (Buell et al. 1971, Bazzaz 1968) but do not achieve increased coverage until much later (Pickett 1982). This pattern may be determined, in part, by competition and predation (Davison and Forman 1982, Armesto and Pickett 1985). Newman et al. (1988) showed that small mammals venture from patch to patch primarily as a function of risk to predation. Small mammals venturing from a mature forest into exposed old fields are at a much greater risk of being killed by higher order predators. Therefore, we hypothesized that small mammalian seed predator-dispersers (e.g., gray squirrels) and seedling browsers (e.g., rabbits and deer) might influence seedling establishment patterns with respect to distance to the forest edge.

We designed an experiment to test the effects of predation, above-ground diffuse competition, and below-ground diffuse competition on woody seedling growth and survival in a five-year-old field that borders an old-growth forest. Specifically, we asked the following questions: (1) What is the relative importance of vertebrate and invertebrate herbivory compared with diffuse plant competition (above- and below-ground) in determining woody seedling establishment and survival in oldfields? (2) Do spatial patterns exist in herbivory, i.e., do differences exist between the forest-field ecotone and the field?

Materials and methods

The study site for this investigation was the Hutcheson Memorial Forest (HMF) research facility, an old-growth mixed *Quercus* and *Carya* forest (Forman and Elfstrom 1975) surrounded by a mosaic of agricultural and abandoned oldfields. HMF is located in East Millstone, New Jersey at 40°30'N by 74°34'W. The silty-loam soils of the area are derived from underlying red shales of the Brunswick formation. Annual precipitation averages ca. 112 cm and is distributed fairly evenly throughout the year. The mean annual temperature is 11.7°C. We used a five-year-old field (dominated by *Aster pilosus, Lonicera japonica, Solidago canadensis*) that borders the forest in our experiment.

Several hundred seeds were gathered from one *Carya tomentosa* (Poir.) Nutt. (Juglandaceae) tree at HMF. The seeds were cold-stratified, germinated, planted in 10 cm pots, and raised in the greenhouse. Seedlings were watered and fertilized regularly. After six months, 80 seedlings were selected to be used in the field experiment based on inspection of their uniformity of height and vigor.

To evaluate the effects of browsers and diffuse competition on seedling survival we designed a stratified two-factor field experiment. Seedlings were planted into a five year oldfield adjacent to the south edge of the forest. Predation was evaluated by enclosing half of the seedlings in wire cages (2.3 × 0.6 × 0.6 m) with the other half serving as controls. Inside and outside cages, diffuse competition was evaluated by three treatments: seedlings planted in 20 cm bottom-perforated pots with in situ (sifted) soil (to remove below-ground competition), seedlings with surrounding vegetation tied back with string (to remove above-ground competion), seedlings both potted and tied (to remove above- and below-ground competition), and control plants receiving no manipulation. Treatment combinations were assigned randomly and replicated 10 times each. All factors were evaluated alone and crossed; by stratifying the plantings into two transects (near forest edge and in the center of the field) we were able to assess the relative influence of forest edge proximity on seedling survival.

Plants were examined approximately every 30 d for two growing seasons, 1987 and 1988. At each evaluation we determined whether the plant was "alive" based on presence or absence of an above-ground stem, what its general condition was, its height (mm), the number of leaflets present, and the relative percent of leaf area lost to invertebrate herbivores (based on a visual estimate). At the end of the second field season we harvested all remaining plants which were alive and partitioned each into root, stem, and leaf biomass fractions. Plants were

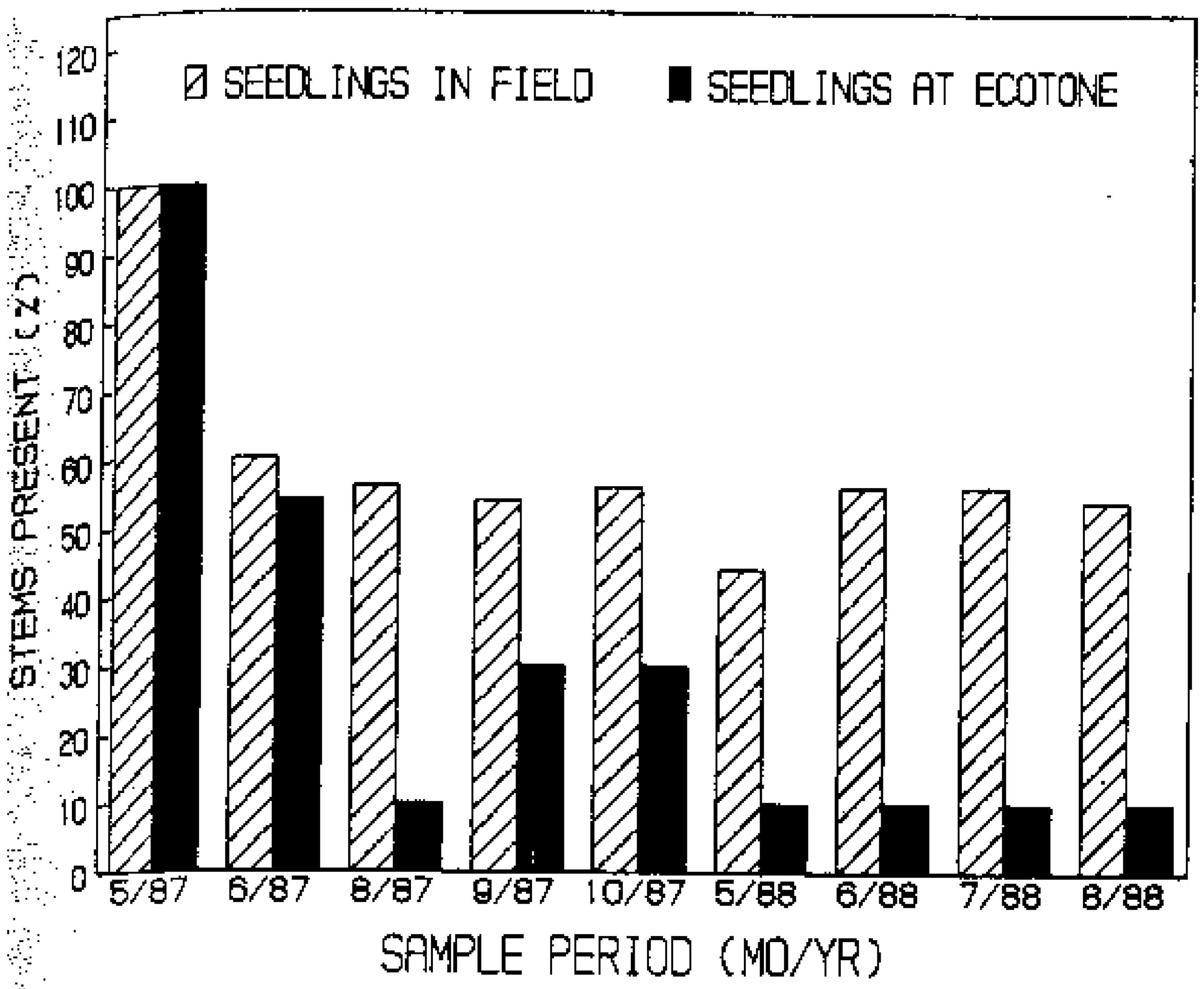

Fig. 2. Proportion of seedlings surviving when at forest-field ecotone vs center of old field. (K-S test, DN = 0.7777, P = 0.0086).

dried at 80°C for 48 h and weighed to the nearest 0.01 g. Plant survival patterns were analyzed using the Kolmogorov-Smirnov (K-S) two-sample test employing STATGRAPHICS (STSC Inc, 1986). Plant height, leaflet number, and biomass were analyzed using the GLM ANCOVA procedure of SAS (SAS Institute, Inc. 1985) where initial plant height was used as the covariate.

Results and discussion

The number of seedlings surviving was strongly influenced (P = 0.0016) by mammalian browsers (Fig. 1). Seedlings not protected from herbivores were consumed almost immediately. During the second year of the experiment, some caged seedlings died apparently due to drought. Resprouting occurred in a number of seedlings after herbivores consumed the above-ground portion of the seedlings early in the season. Thus, the number of stems increased in certain sample periods (Fig. 1). Some of the seedlings were observed to resprout up to two times in the same season. Monk (1981) showed that early survival of mockernut hickory in a southeastern U.S. oak forest was best described by a negative exponential model. Our data suggest that herbivory probably accounts for the majority of early mortality.

We tested the hypothesis that distance to the forest edge influenced herbivore behavior; we examined spatial herbivory patterns by comparing the survival of unprotected seedlings at the forest edge vs the field center. Seedlings away from the forest (by 15 m) had greater survival than those next to the forest (within 5 m, Fig. 2; P = 0.0086). The resulting seedling shadow, thus, represents a resolution between two conflicting forces: a leptokurtic distribution of seeds and seedlings at the forest edge opposed by heavy predation at the edge. Seedling survival apparently increases when seedlings can escape predation associated with the ecotone. This may be a terrestrial example of a browse zone where grazers forage at a set distance from the surrounding matrix (Sousa 1984).

Because only a few seedlings survived in uncaged treatments, we examined only the caged seedlings to determine the effects of our competition treatments. Fig. 3 illustrates the biomass of caged seedlings harvested at the end of the experiment. No significant (P > 0.05) trends were observed in leaf, stem, root or total biomass among competition treatments. Neither were significant (P > 0.05) differences found for stem height and number of leaflets over time. Seedlings without above-ground competition (i.e., no shading by neighbors) appeared to suffer greatly during drought in the second growing season, which eliminated a trend towards greater growth for those seedlings observed in 1987. Other studies have found that root competition was often more intense than shoot competition and that the relative importance of root competition may increase with time (Wilson 1988).

During the first growing season (1987) 15% of the seedlings had an average of 10% of their total leaf area consumed by invertebrates. During the second growing season (1988) 30% of the seedlings showed damage. The damage was primarily in the 1% to 10% range. No seedling suffered enough insect herbivory to kill it or obviously affect its growth. Phytophagous insects probably have little effect on plant survivorship relative to mammalian browsers (Crawley 1983) except at times of great insect population increases.

Conclusions

We found whole-plant browsing by mammals to be the primary cause of woody seedling mortality in the old-

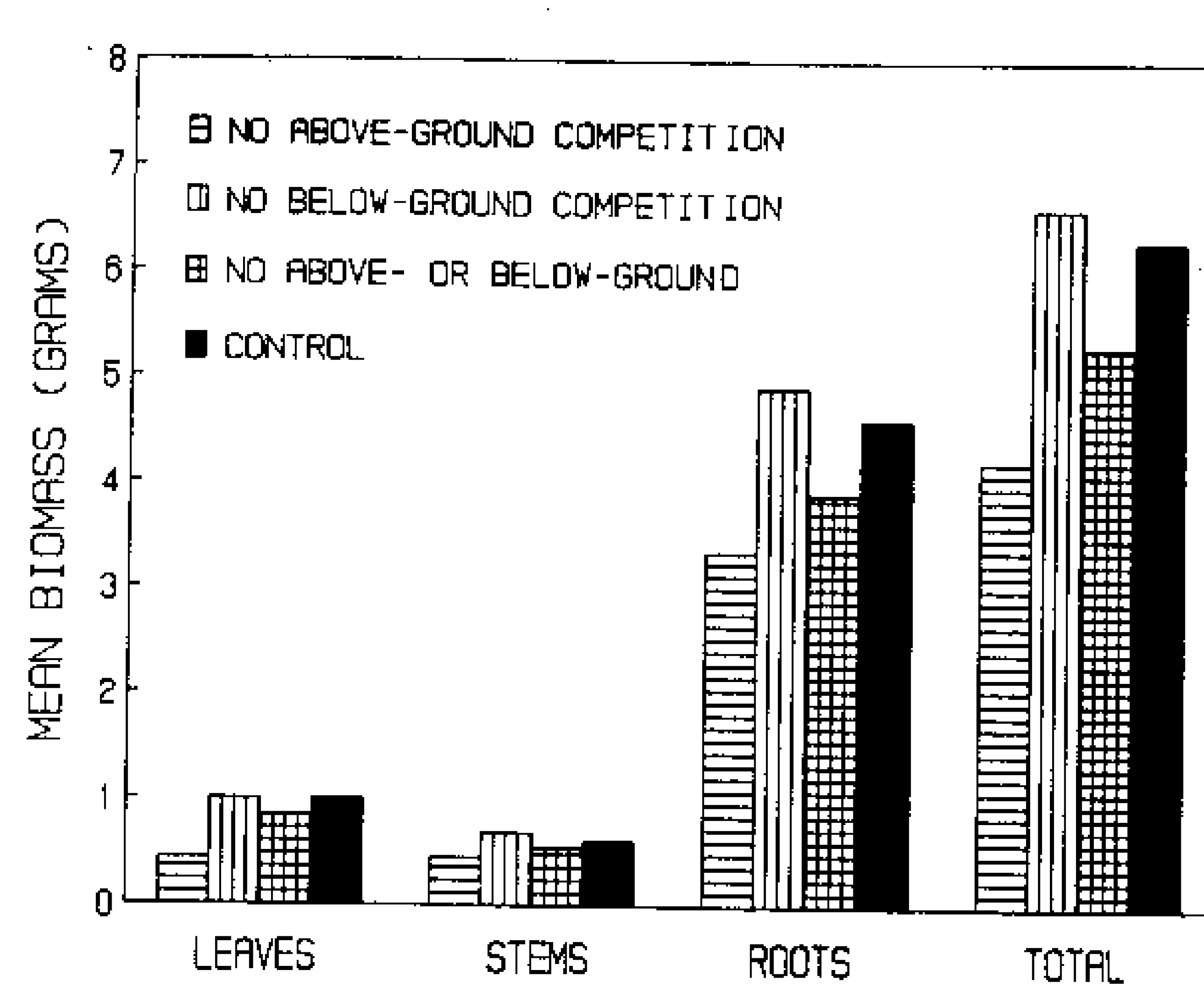

Fig. 3. Partitioning of biomass for seedlings grown under four competition scenarios. Treatments are not significantly different (ANCOVA, P > 0.05) among biomass elements.

field studied. Apparently, predation does not change competitive relationships, rather it defines if competition can occur at all. Herbivores consumed almost all uncaged seedlings. Those few seedlings that survived did not belong to similar competition treatments. Many species of woody plants may overcome the long-term effects of browsing by resprouting. Presumably a seedling may escape predation and grow past a threshold size whereby it is no longer susceptible to whole-plant browsing, i.e., reaches a size refugium.

Herbivory clearly defines tree seedling establishment and survival. Competition may affect growth and survial if given a chance to operate. In that case, herbivory would act as a filter for future competitive interactions. This view departs from the traditional 'single mechanism' view of community dynamics and succession (e.g., Connell and Slatyer 1977) and is consistent with a multimodel view of predation and competition acting in concert (Menge and Sutherland 1976).

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