

Arthropod Biodiversity in Succession: Separating the
Effects of Litter Depth and Composition

by

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Literature Review

The rapid expansion of human activity has caused drastic changes in the structure, dynamics, and biodiversity of the earth's ecosystem, and because of the unprecedented nature of this expansion, there is little historical information to fully prepare us for its impacts (Tilman, 1990). In the absence of historical information, an understanding of the ways in which communities respond to perturbations and an understanding of the mechanisms that maintain biodiversity within communities is needed to provide some insights into the ramifications of human disturbance on the ecosystem and to provide the tools needed for conservation of biodiversity.

When an ecological community is subjected to natural perturbation, such as fire, flooding, and drought, and unnatural perturbation such as clear-cutting, its subsequent dynamics of change are called successions (Tilman, 1990). Successions that occur on newly exposed landforms are referred to as autogenic successions. If the exposed landform has not been previously influenced by a community, its subsequent pattern of autogenic succession is referred to as primary succession, but if the exposed landform has well-developed soil, seeds, and spores remaining, secondary succession follows. Successions following freshly formed land dunes, lava flows, and pumice plains caused by volcanic eruptions (Del Moral, 1998) are examples of primary succession, while those following the loss of trees as a result of disease, fire, or clear-cutting are examples of secondary successions.

Our experiment involved the successional dynamics following clear-cutting, a common silvicultural practice. One of the main problems with clear cutting is its elimination of many rare species associated with old-growth forests (Niemela, 1997; Kaila et al., 1997). Most of these rare old growth specialists go locally extinct from the immediate environmental trauma of clear cutting, and the remaining become extinct in following successional stages. The survivors of the initial trauma are unable to reproduce in the dryer early stages that follow clear cutting, and the destruction of suitable habitat patches, caused by the cutting down of trees, also leads to their increased isolation. The survivors of the initial clear-cutting are thus forced from metapopulation

extinction safeguards and the likelihood of recolonization after a local extinction decreases (Niemela, 1997).

Although many studies have found a decrease in old growth specialists following clear-cutting, many have also found increased general diversity in recently clear-cut forests (Butterfield, 1997; Paquin and Coderre, 1997). Butterfield (1997) found that both diversity and individual density were highest in young plantations and lowest in the old plantations. Setälä and Marshall (1994) have attributed this increase in diversity in the early stages following clear-cutting to the "refugium" created by the decomposing tree stumps, while Niemela (1997) has attributed this early increase of diversity to the fact that tree-living species thrive on the open and dry conditions that follow clear cutting. Atlegrim and Sjöberg (1995) agree with Niemela in attributing this increased diversity to changes of abiotic factors like increased temperature and indirect effects like increased sun exposure following clear cutting which affect food plant quality for herbivorous. Kaila et al. (1997) have even found several beetle species that can only be found in clear-cuts associated with open forest habitats, such as burned forests or storm-damaged areas. They concluded that dead trunks left in the clear-cut areas may host not only generalist epixylic species but also many beetle species specialized to warm, sun exposed environments who may not be able to survive in closed forests.

Black Rock Forest, where our study was conducted, is located in the Hudson Highlands of New York, approximately 2 km west of the Hudson River and 80 km north of Manhattan, and the successional trends at Black Rock follow those of the Hickory-Oak forests that extend from Massachusetts to Ohio. As succession proceeds in such forests, the leaf litter depth increases while the diversity of leaves that compose the leaf litter decreases. The leaf litter depth pattern occurs because of accumulation of leaves on the ground over the years. The leaf litter diversity pattern occurs because the initial invaders of the newly clear cut plot are generally r-selected species who are generally poor competitors and, therefore, depend primarily of their fast reproductive rates for survival. Numerous r-selected species can invade a community at once. They put all their energy into reproduction and none into defense, and numerous r-selected species can be found in any new

environment. Because they produce a lot of diverse leaf litter which contains little or no secondary chemicals and is palatable to numerous litter arthropods, the presence of the r-selected species is often accompanied by an increase in leaf and litter arthropod diversity.

As succession advances, the better competitors, the K-selected species overtake the r-selected species. K-selected species are only limited by their carrying capacity. They do not reproduce as quickly as the r-selected species because they put more energy into their defense. Their numbers in a community are smaller and so is their diversity. The leaf litter they produce is, therefore, not only less diverse, but it also contains more secondary chemical components: resins, terpenes, lectins, alkaloids, and tannins which make it less palatable to litter arthropods. Their presence is generally accompanied by a decrease in litter arthropod diversity.

Although successions on newly exposed landforms typically take several hundreds of years to run their course, and the research life of an ecologist is not sufficient to encompass such a time span, there are ways to gain information about the successional patterns of such long time scales. Sometimes successional stages in time can be represented by different communities in space. For instance, a series of communities currently in existence, but corresponding to different lengths of time since the onset of succession, can be inferred to reflect succession (Tilman, 1990). Ecological succession was first recognized in plants on sand dunes by Cowles (1899) because, as sand piled up against a lake or seashore, its successional changes were stratified in space, from the new ground directly in front of the water awaiting colonization to the oldest successional stage farthest from the water.

Succession has long intrigued ecologists not only because successional trends are so pervasive in nature, but also because of the repeatability of successional dynamics and the broad similarities among successional sequences in a wide range of habitats (Tilman, 1990). A model of succession which seems to be capable of generating quite accurate predictions has even been developed by Horn (1975). This matrix model predicts changes in tree species composition in a hypothetical forest, and always converges on a stationary, stable tree composition that is independent of the initial composition of the forest.

The pervasive, repeatable, and generally consistent nature of succession makes its study vital to the establishment of theories that can explain the maintenance and recovery of biodiversity. Because of this utility of successional patterns, many descriptive studies have been done on succession following many types of disturbances in different habitats. Del Moral (1998) has described the early succession of larches spawned by Mount St. Helens, Sousa (1979) has described the successional pattern of algal species that colonized concrete blocks introduced to an intertidal zone, and countless others have described succession in other habitats (Stockey, 1994; Zmarzly et al., 1994). However, the conservation of biodiversity in the face of the escalating global changes of today, requires a much fuller understanding of the forces behind the maintenance and recovery of biodiversity. Most of the qualitative successional studies that have been done have fallen short of the orderly mechanisms behind the successional pattern, and have instead focused only on describing the successional pattern (Callan, 1964; Martin, 1966).

My project aimed to increase understanding of the trends of succession by delving into the mechanisms behind the successional trend. I studied two of the factors that influence biodiversity in the successional stages following clear-cutting, specifically the influence of leaf litter depth and leaf litter composition on arthropod diversity. There have been previous studies conducted on the trends in arthropod biodiversity through succession following clear-cutting, and the observed trend in general litter arthropod diversity is a rapid increase in diversity through successional time (climaxing at around 30 years) and then a decline until the climax community, when diversity levels off (Danoff-Burg & Bird, unpublished data). Unfortunately, these studies have also conflated the individual effects of leaf litter composition and leaf litter depth on arthropod diversity.

Species diversity is a quantitative ecological characteristic, unique to the community level of organization, which has been applied to three different kinds of relationships. Alpha diversity, the central relationship, refers to the diversity of species within a given habitat. Beta diversity describes the degree of change in species from one habitat to another, and gamma diversity relates to the total regional species diversity that results from the number of habitats present, the diversity of species within each, and the degree of turnover of species between habitats (Huston, 1994). Our

project dealt primarily with alpha and beta diversity since we not only looked at both the diversity of the old-growth and new-growth plots individually but also the relative diversities of the two plots.

Another important underlying theory behind our project was the concept that increasing the depth of leaf litter available increased the overall quantity and variety of niches, while increasing diversity of leaf litter increased the variety of available niches without increasing the overall quantity of niches. The concept of the niche to describe the place of an organism in the environment was first introduced by Grinnell in 1971 (Huston, 1994). Because species adapt to exploit a certain set of necessary resources, and those with closely similar requirements compete for them, the resources directly available in a community influence the number of species in the community and their relative abundance (Price, 1997). In other words, the available niches in a community determine its diversity and abundance of species.

Unfortunately the arthropod niche has largely been overlooked in previous descriptive successional studies. These studies have narrowly focused on the diversity of plants and their herbivores and not on predatory arthropods. However, in a review of invertebrates and boreal forest management, Niemela (1997) noted the potential utility of invertebrates as a "surrogate for diversity". One such potentially useful surrogate for diversity is the soil and litter arthropod. Through their influence on decomposition, nutrient cycling, and energy transfer, soil and litter arthropods form an integral part of the forest ecosystem, and can, therefore, be used as a valuable gauge of shifts in general forest succession and biodiversity.

In our experiment, we strove to separate the mechanisms of leaf litter depth and leaf litter composition from the arthropod diversity trend by teasing apart the effects of the different leaf litter depths and compositions of an 11 year old and a 96 year old.

Abstract

Most previous studies have conflated the individual effects of leaf litter composition and leaf litter depth on arthropod diversity through succession. This experiment aimed to tease apart these two forces that together determine arthropod diversity during succession. Two adjacent and comparable plots, one clear-cut 11 years and the other clear-cut 96 years prior to the study, were used in a mixed hardwood forest in Cornwall, New York, and three sets each of four different treatments of varying leaf litter composition and leaf litter depth were placed in both plots and left for six weeks.

After sorting and analyzing the four treatments, we found that deeper litter treatments were always more diverse than thinner litter treatments, and that within a depth treatment, those bags with the same leaf litter composition as the surrounding litter were the most diverse. We concluded that litter depth is the main determinant of arthropod diversity through succession, but that local adaptations also influence diversity.

Keywords: succession, biodiversity, clear-cutting, arthropods, leaf litter depth, leaf litter composition

Introduction

The rapid expansion of human activity has caused drastic changes in the structure, dynamics, and diversity of the earth's ecosystem, and because of the unprecedented nature of this expansion, there is little historical information to fully prepare us for its impacts. In the absence of historical information, an understanding of the ways in which communities respond to perturbations and an understanding of the mechanisms that maintain biodiversity within communities is needed to provide some insights into the ramifications of human disturbance on the ecosystem and to provide the tools needed for conservation of biodiversity.

When an ecological community is subjected to natural perturbation, such as fire, flooding, and drought, and unnatural perturbations such as clear-cutting, its subsequent dynamics of change are called succession (Tilman, 1990). Succession has long intrigued ecologists because successional dynamics are somewhat repeatable and there are broad similarities among successional sequences in a wide range of habitats. The study of successional patterns is also vital to the establishment of theories that can explain the maintenance and recovery of biodiversity. Many descriptive studies have been done on the successional patterns following many types of disturbances in different habitats. For instance, Del Moral (1998) has described the early succession of larches spawned by Mount St. Helens, Sousa (1979) has described the successional pattern of algal species that colonized concrete blocks introduced to an intertidal zone, and countless others have described succession in other habitats (Stockey, 1994; Zmarzly et al., 1994). However, the conservation of biodiversity in the face of the escalating global changes of today, requires a much fuller understanding of the forces behind the maintenance and recovery of biodiversity. Most of the qualitative successional studies that have been done have fallen short of the orderly mechanisms behind the successional pattern, and have instead focused only on describing the successional pattern (Callan, 1964; Martin, 1966).

My project aimed to increase our understanding of the trends of succession by delving into the mechanisms behind the successional trend. I studied two of the factors that influence biodiversity in the successional stages following clear-cutting, specifically the influence leaf litter depth and leaf litter composition on arthropod diversity. There have been previous studies done on the trends in arthropod biodiversity through succession (Danoff-Burg & Bird, unpublished) but these studies have also conflated the individual effects of leaf litter composition and leaf litter depth on arthropod diversity. The importance of studying the effects of changes in both leaf litter depth and leaf litter composition is significant because leaf litter depth and leaf litter composition independently contribute to changes in alpha diversity in unique manners. Increasing the depth of leaf litter increases the overall quantity and variety of niches available. In contrast, increasing

diversity of leaf litter increases the variety of available niches, but not the overall quantity of niches.

Most previous descriptive successional studies have narrowly focused on the diversity of plants and their herbivores and not on predatory arthropods. In a review of invertebrates and boreal forest management, Niemela (1997) noted the potential utility of invertebrates as a "surrogate for diversity", and one such potentially useful surrogate for diversity is the soil and litter arthropod. Through their influence on decomposition, nutrient cycling, and energy transfer, soil and litter arthropods form an integral part of the forest ecosystem, and can, therefore, be used as a valuable gages of shifts in general forest succession and biodiversity.

In this experiment, we strove to separate the mechanisms of leaf litter depth and composition from the arthropod diversity trend by teasing apart the effects of the different leaf litter depths and compositions of 11 year old and a 96 year old forests.

2. Methods

2.1. Description of Study Site

We conducted a leaf litter manipulation project on 2 plots in Black Rock Forest which is a mixed hardwood forest located in Cornwall, New York in the Hudson Highlands of New York, approximately 2 km west of the Hudson River. The tree species composition at Black Rock is typical of the Hickory-Oak forest that extends from Massachusetts to Ohio.

Past data collected at Black Rock Forest (Figure 1) by Danoff-Burg and Bird (unpublished data) showed that arthropod diversity in succession following clear cutting peaked around 30 years, then declined, and leveled off to the climax community.

The 2 sites chosen for this project were adjacent old and new growth sites, separated by a low traffic volume dirt road. The old growth site had been clear cut 96 years before this project and was predominantly composed of red maple. The new growth site had been clear cut 11 years

before this project and was predominantly composed of blueberry, ferns, and moss, and was surrounded by a diversity of oaks species which contributed greatly to its leaf litter content.

2.2 Trapping Methods

We sampled the arthropod diversity using 0.30 m x 0.46 m leaf litter bags made of chicken wire (with 0.019m mesh). We used 4 different sets of treatments with all possible combinations of 2 litter depths and 2 litter compositions, such that the first set of bags contained 2.5 kg of leaf litter that had been collected from the older site, the second set contained 0.45 kg of leaf litter also from the older site, the third set contained 2.5 kg of leaf litter that had been collected from the newer site, and the fourth set contained 0.45 kg of litter also from the newer site. There were three replicates of each of the 4 treatments in each of the two sites (Figure 2). The two sites were laid out in a Latin square which maintained an even distribution of all the treatments throughout the sample sites and controlled for any variation in diversity based on proximity to the roads or other natural variations in the forest. The 0.30 m x 0.46 m area under each bag was first cleared before each bag was put down. The bags were nailed down to keep them in place and to standardize the degree of leaf litter packing in all the litter bags.

The bags were kept in the forest to collect arthropods for 6 weeks (from 19 June to 31 July, 1998) then removed. The arthropods within the bags were collected using Berlese funnels then sorted to morphospecies.

2.3 Data Analysis

We analyzed the data using raw diversity counts, Shannon (Peet, 1974; Pielou, 1977) and Simpson (1949) diversity indices to measure the heterogeneity of the two sites, Hill's Evenness, and Jaccard and Morisita-Horn (Horn, 1966) similarity indices to measure community similarity.

3. Results

We collected 5169 individuals from the leaf litter bags in the old site and 7345 individuals from the litter bags in the newer site. These individuals included parasitic wasps, flies, plant bugs, spiders, springtails, beetles, ants, mites, and other arthropods.

The thick leaf litter consistently showed greater arthropod diversity than the thin leaf litter. The thick old litter from both the older and the younger sites was more diverse than the thin old litter and the thin new litter from both the older and the newer sites. The thick new litter from both sites was also more diverse than the thin old litter and the thin new litter from both sites. When we looked at the two sites separately, we found that together the thick litter bags in the older site (regardless of composition) contained an average of 39.5 more morphospecies than the thin litter bags of that site, and that together the thick litter bags in the younger site contained 65.5 more morphospecies than the thin litter bags of that site.

In the old growth site, diversity was greater in the leaf litter originally collected from the old growth site than in the leaf litter bags of the same size originally collected from the new growth site (Figure 3). We retrieved 105 morphospecies from all the thick old litter bags compared to 63 morphospecies in the thick new litter bags. We also found 58 morphospecies in the old thin litter bags compared to 31 morphospecies in the new thin litter bags. So of the bags left in the old site, the thick old litter bags showed the greatest diversity, followed by the thin old bags, then the thick new bags, and finally the thin new bags.

In the new growth site, we found diversity to be greater in the leaf litter originally collected from the new growth site than in comparable sized litter bags originally collected from the older growth site. We retrieved 78 morphospecies from the thick new litter compared to 74 morphospecies in the thick old litter bags. Although this difference is not great, a greater difference would have probably been seen if more samples had been taken because there was consistently a greater number of species in the thick new litter bags compared to the thick old litter bags. There

were 21 morphospecies in the thin new litter bags compared to six in the thin old litter bags. The trend in diversity in the litter bags retrieved from the new growth site was that new thick litter bags had the greatest diversity, followed by new thin litter, then thick old growth litter, and finally thin old growth litter.

These trends caused by differing leaf litter compositions were further supported by the fact that together all the old litter bags in the older site, regardless of depth, contained 34.5 more morphospecies than the new litter in the older site, and that all the new litter in the newer site contained 9.5 more morphospecies than the old litter in the newer site. This data also shows that the difference in diversity caused by varying leaf litter composition is much greater in the older site than it is in the younger site. Although the organisms in the new growth forest slightly favored the new growth litter bags to the old growth bags, the organisms in the older showed a much stronger preference for the old growth bags over the new growth ones.

We are limited in our interpretation of the individual effects of leaf litter depth and composition on arthropod diversity by the limited number of replicates of each of the treatments. More replicates would be needed to make more conclusive interpretations. We would also need to have collected more information about the diversity at more intervals of time following clear-cutting to truly observe the effects of varying leaf litter depths and compositions through the continuum of succession. Because we only looked at diversity in two time periods following clear-cutting (85 years apart), we cannot deduce the short term and continuous variation in arthropod diversity due to changes in leaf litter depth and composition.

4. Discussion

We show that a major key behind the successional trends in biodiversity is simply leaf litter depth. Deeper leaf litter consistently contained a more diverse community of arthropods than thinner litter, and since just increasing the leaf litter depth only increases the space in niches but not the variety of niches, our results show that increasing the space in niches allows more species to

coexist in each niche. This contradicts the generally accepted theory that species cannot exploit the same niche and coexist, however, increasing the leaf litter depth may have effectively introduced sufficient microhabitat differences within the leaf litter to permit coexistence of species. There have been other cases in which microhabitat differences have been shown to be sufficient in permitting coexistence. O'Neill (1967) found seven species of diplopod coexisting in decaying material in maple-oak forests in central Illinois, and concluded that each was dominant in only one of seven microhabitats: heartwood at center of logs, superficial wood of logs, outer surface of logs beneath bark, under log but in log surface, under log but on ground surface, within leaves of litter, and beneath litter on ground surface. Tahvanainen (1972) also showed the implementation of microhabitat partitioning in two congeneric flea beetles on crucifers, *Phyllotreta cruciferae* and *P. striolata*, which occupy different surfaces of *Brassica oleracea* leaves. In his study of species of *Erythroneura*, McClure (1974, 1975) (McClure & Price, 1975, 1976) found different species distributed along a latitudinal gradient with each species better adapted to one point of latitude than the other species, and he too concluded that geographical distributions of the species differed sufficiently to enable coexistence, and that even though niche differences were not significant, habitat differences were sufficient for coexistence.

Price (1971) also showed that three species of ichneumon were able to survive together because of different responses to habitats defined by moisture content in the litter and host density, and Turnbull (1966) found a similar response in which the lycosid spiders *Pardosa milvina* and *P. sexatilis* showed niche segregation on a moisture gradient. The niche segregation of the arthropods in our study could have similarly been along a moisture gradient since the leaf litter at the bottom of the litter bags (especially the thicker bags) retained more moisture than the litter at the tops of the bags. However, there could also have been any of a number of other gradients established in the leaf litter bags including gradients based on exposure to sunlight and air, and future experiments should definitely check for such gradients.

Secondary to the effect of leaf litter depth, we showed that arthropod adaptations to the leaf litter composition of their local environment also play a role in determining diversity. The leaf litter

originally from a site attracted more arthropods than foreign leaf litter placed in that site. This supports the theory that species adapt to exploit a certain set of necessary resources, and are then able to compete best for that niche. This data also corroborates the intrinsic differences in adaptability among species that colonize an old growth forest compared to those that colonize a new growth forest. Our data showed a stronger preference of the arthropods in the old growth site for leaf litter bags containing old litter than was shown for new litter by the arthropods in the newer growth site. This occurred because the old growth forest is generally colonized by many old growth specialists with very narrow adaptations for the old growth forest while the new growth forest generally attracts generalists capable of exploiting different resources. It is important to note, however, that there was some preference for the new growth litter bags shown by the arthropods in the newer site which supports the findings by Kaila et al. (1997) of several beetle species that specialize in new clear-cut forests.

Our results support the findings of other papers stating the importance of maintaining forests of varying ages (Niemela, 1997), but they uniquely point to some of the reasons behind the importance of varying ages of forests, namely varying depths of leaf litter and varying litter composition. But these are just two of the mechanisms behind successional biodiversity. It is, therefore, important to determine through more quantitative successional studies, the roles of other driving mechanisms such as humidity, sunlight, and other abiotic factors on successional biodiversity.

Acknowledgments

I would like to thank Margaret McDonald, Stephanie Biedermann, Jamie Ballantyne, Katherine Pease, Young Chae, Bess Kwok, and Shanta Duffield for their help in collecting and sorting the experimental samples; William F. Schuster for providing us access to The Black Rock Forest; Simon Bird for his help with the diversity analyses; and the Howard Hughes Medical Institute and the Biology Department of Barnard College for funding this project.

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Figure Legends

Figure 1. Arthropod Diversity Through Successional Time at Black Rock Forest. Bars show average number of species in found each age of plot. Diversity has been found to peak around 30 years.

Figure 2. Sample Site Layout. Sites are lain out in a Latin square to maximize distribution of treatments. Two sites are separated by 9 m of a low traffic volume dirt road. Sample in a linear transect are separated by 3 m and sub-samples are separated by 1m.

Figure 3. Diversity of Experimental Treatments in Relation to Age of Plot. Total number of species found in each treatment in each plot. Data is further subdivided into smaller arthropod categories represented by various colors.

Figure 1

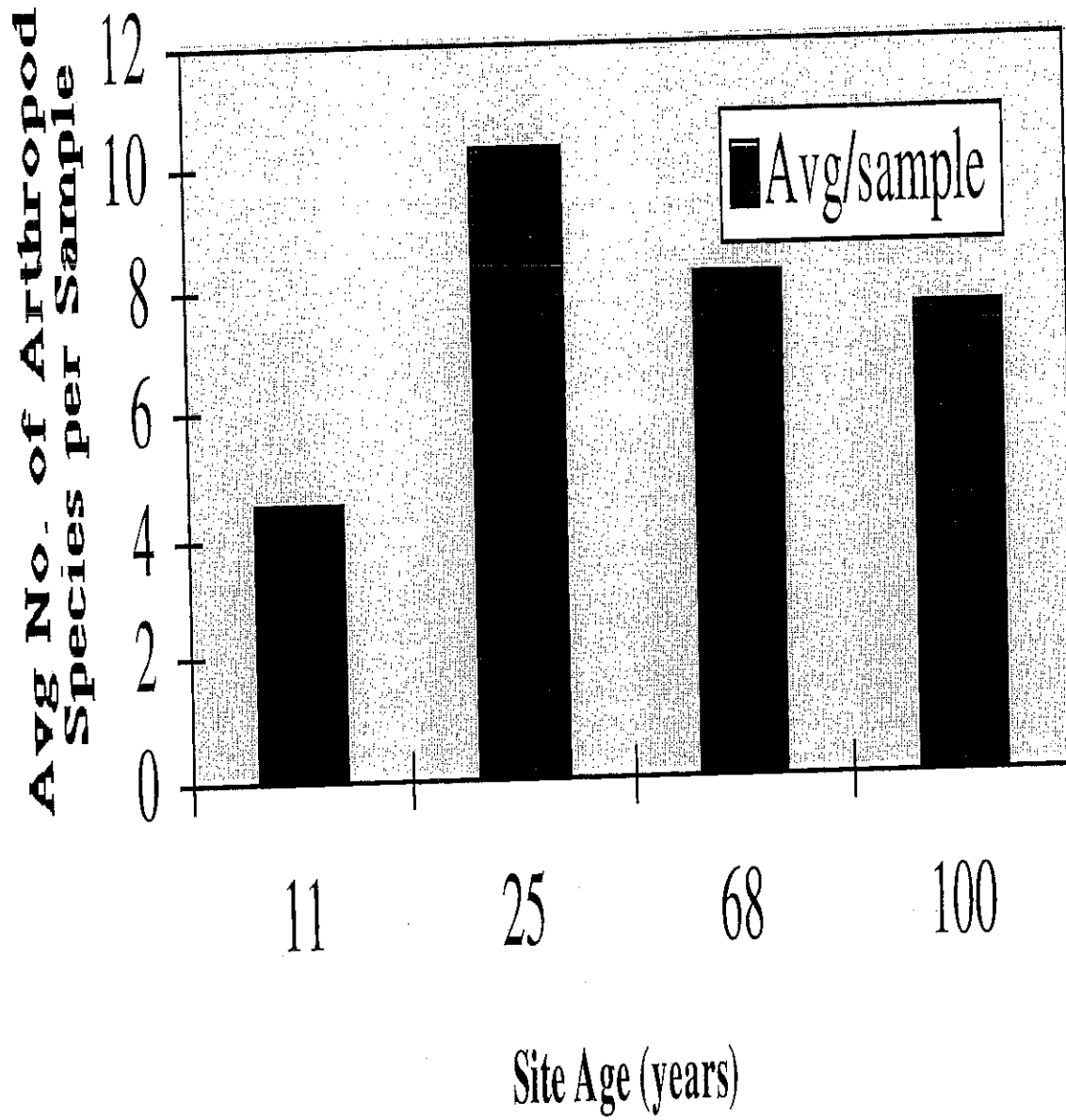
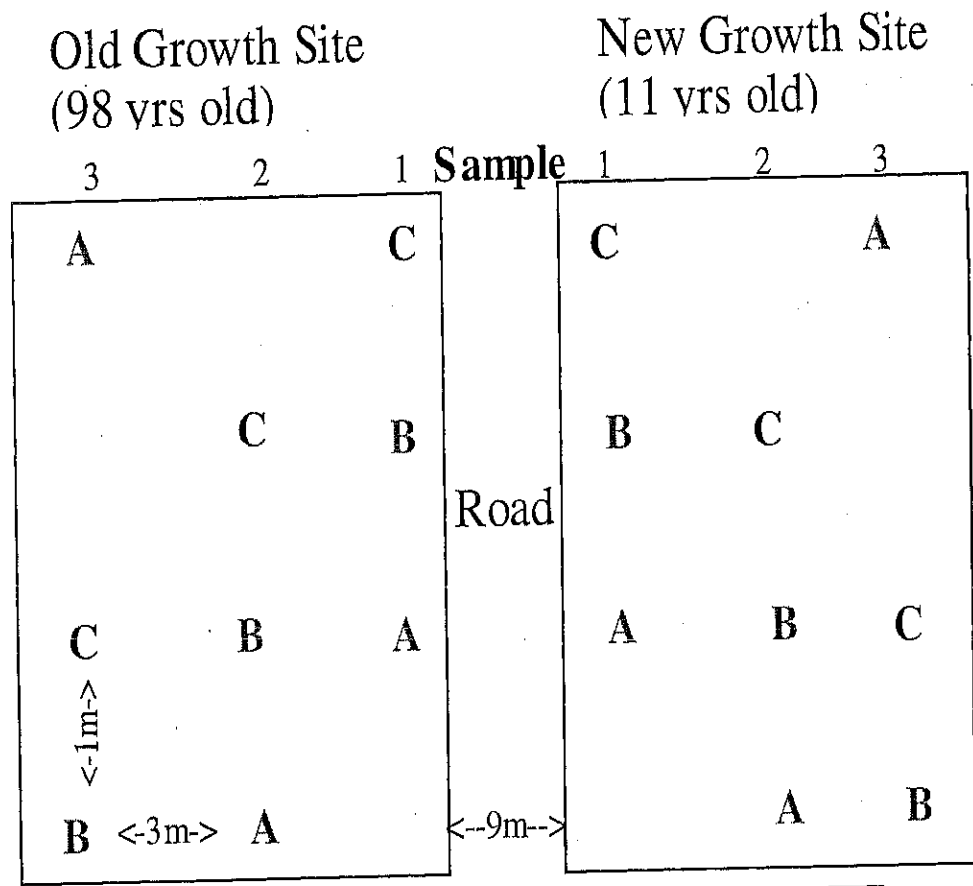


Figure 2



A = old site thick depth
 B = old site thin depth
 C = new site thick depth
 ○ = new site thin depth
 thick depth contains 5.5 lbs of leaf
 litter thin depth contains 1 lb of leaf litter

Figure 3

