RESPONSE OF SOIL MICROARTHROPODS AND MICROCLIMATIC CONDITIONS TO TWO-AGE REGENERATION IN HARDWOOD FORESTS IN THE SOUTHERN APPALACHIANS

by

STEPHANIE LEE MADSON

(Under the Direction of DAVID C. COLEMAN)

ABSTRACT

Forest stands are harvested on a scale of several hectares, whereas most microarthropods will spend their entire lives within a scale of several meters. Rarely is this mismatch between spatial scales accounted for when examining the response of soil microarthropods to forest harvesting methods, such as two-age regeneration treatments. Microhabitats, i.e. residual trees, coarse woody debris piles, grassy clearings, residual shrubs, coppices, and skid roads, are created or exacerbated by the harvesting process. Microhabitats have been shown to be a determining factor in microarthropod community composition. Microclimatic conditions, including soil temperature, soil moisture, bulk density, and litter depth, are also determinants of microarthropod community composition. We measured microclimatic conditions and used microhabitats as a common spatial unit to assess the response of soil microarthropods to two-age regeneration treatments within hardwood stands at Wine Spring Creek Watershed in the southern Appalachians. Soil temperature was measured using Hobo data loggers and soil water content was measured using the gravimetric method. Microarthropods were extracted using modified Tullgren extractors and sorted to sub-order. Natural spatial heterogeneity in the soil microarthropod communities was high in both the control and cut sites. Soil microarthropod abundance decreased in the two-age regeneration treatments, with the exception of the immature oribatids, which increased, and the oribatids, which were not significantly different between treatments. Two-age cut stands had significantly greater fluctuations in soil temperatures, higher soil temperatures in summer, cooler soil temperatures in winter, decreased litter depth, and a trend towards decreased soil water content. Understanding of microarthropod community dynamics in response to harvesting was broadened when examined at the scale of microhabitats. Microarthropod abundance was lowest in skid roads and was highest in coppiced and mature tree microhabitats. Using microhabitats as a common spatial scale between microarthropod taxa and harvested forest stands appears to be a useful tool in elucidating treatment effects on the dynamics of microarthropod communities.

INDEX WORDS: Soil microarthropods, oribatids, collembola, mites, myriapoda, spiders, insects, protura, pseudoscorpions, two-age regeneration, forest harvesting, hardwood forests, spatial scales, microclimate, soil temperature, soil water content, organic matter, leaf litter, bulk density, southern Appalachians

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DEDICATION

To the many friends
who have supported me through this process
and to the many who are as family.
Your love, support, encouragement,
and, in some cases, elbow grease,
have been very important to my success
(*sensu* Emerson).
I am blessed.

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CHAPTER 1

INTRODUCTION

In North America, it is estimated that approximately 121 million hectares of forest were cleared between the arrival of Europeans and the early part of the 20th century. Since 1945, forest biomass has increased in the United States through the growth of secondary forests and the reforestation of abandoned agricultural lands (Williams 2003). As forest biomass has increased in the United States, public controversy about policy and management practices on public forest lands has also increased. In the late 1980s, the claims of commercial timber companies versus those of biodiversity advocates came to a head in the Pacific Northwest in the debate over the spotted owl and old-growth ecosystems. The result was nationwide shifts of policy and management goals for federal agencies charged with the management of public forest lands. Management has shifted in recent years away from clear-cutting towards an increase in selective harvest and other regeneration methods in an attempt to meet the multiple goals of maintaining ecosystem processes, maximizing species diversity, and maintaining habitat structure, while continuing timber production (Caza 1993, Franklin 1993, Hopwood 1991, McComb *et al.* 1993).

Silvicultural practices reduce stand density through the partial removal of the overstory canopy. These practices, known collectively as regeneration treatments, have been recognized as the primary tool for land managers to meet the specific objective of producing habitat and maintaining species diversity, while continuing timber production

(Cole 1996, FEMAT 1993, Tappeiner 1992). Regeneration treatments release the remaining trees from crowded stands, allowing the trees to grow larger and healthier. Site regeneration is enhanced and occupancy by plant species hitherto restricted to other habitats is facilitated. As plant diversity increases, it is expected that faunal diversity will follow.

Arthropods are integral to a functioning forest ecosystem and perform key roles as detritivores, herbivores, predators and prey. Microarthropods, in particular the oribatid mites (Acari: Oribatida), are the most abundant and diverse animals living in soil and litter environments. Soil and litter arthropods aid in the regulation of rates of nutrient cycling, decomposition, and energy flow (Petersen and Luxton 1982, Wallwork 1983, Seastedt 1984, Persson 1989, Wardle and Giller 1996). Disturbance of microarthropod communities has the potential to alter or disrupt these essential ecosystem processes.

The goal of this study is to characterize the response of soil microarthropod communities and microclimatic conditions to two-age regeneration within hardwood stands in the southern Appalachians. The effect of regeneration methods on microclimatic conditions is only beginning to be examined in a wide variety of forest ecosystems. The goal of the first paper is to characterize the effect of two-age regeneration on microclimatic conditions, which in turn influence soil microarthropod community dynamics. Our objectives are to (*i*) compare landscape changes in microclimatic conditions between two-age regeneration stands and controls, and (*ii*) compare local changes in microclimatic conditions among microhabitats created by the harvesting process. We hypothesize that two-age regeneration methods will increase soil temperature, will decrease soil water content, and decrease litter depth in stands. We hypothesize that the skid road microhabitat will have the greatest bulk density from compaction caused by skidding, the warmest soil temperatures since it has no canopy cover, and show the greatest variation in soil temperatures since it is the most exposed. We hypothesize that the mature tree and coppice/shrub microhabitats will have the lowest bulk density since harvesting operations would have been less concentrated near residual trees and shrubs, cooler soil temperatures due to the intact canopy cover, will exhibit the least variation in soil temperature for the same reason, and the greatest accumulation of litter. We hypothesize that the coarse woody debris microhabitat will have the highest soil water content since there will be little moisture uptake by vegetation in that microhabitat.

In the second paper, the effect of two-age regeneration on the abundance and distribution of litter-dwelling soil microarthropods is characterized. The objectives of the second paper are multifold. The first objective is to establish the natural variation and spatial heterogeneity within microarthropod communities of undisturbed forest stands. The second objective is to compare the abundance of microarthropod communities within control sites to regeneration stands. The third objective is to establish the correlation between microarthropod communities and microhabitat types. It is hypothesized that mature trees and coarse woody debris will have the highest abundance of microarthropods, that coppices, shrubs and herbaceous clearings will have a relatively lower abundance of microarthropods compared to the previous microhabitat types, that the herbaceous clearings and woody debris piles will yield distinct community assemblages from the other microhabitats, and, lastly, that skid roads will have the lowest abundance of microarthropods. The fourth objective is to correlate differences in abundance and distribution of microarthropod assemblages with measured explanatory variables (soil temperature, soil water content, bulk density, litter depth).

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CHAPTER 2

LITERATURE REVIEW

Spatial and Temporal Distribution of Soil Microarthropods

Introduction

Microarthropods, in particular the oribatid mites (Acari: Oribatida), are the most abundant and diverse arthropods living in soil and litter environments (Brussaard *et al*. 1997). Soil microarthropods are attributed with regulating many soil processes, including decomposition, mineralization, populations of other soil organisms, energy flow, and nutrient cycling in ecosystems (Persson 1989, Petersen and Luxton 1982, Seastedt 1984, Wallwork 1983, Wardle and Giller 1996). Disturbance of soil microarthropod communities has the potential to alter or disrupt these processes.

Natural disturbances and anthropogenic alteration of the landscape affect soil microarthropod communities. Fire drastically reduces the numbers of microarthropods (Huhta *et al*. 1967, Huhta *et al*. 1969, Vlug and Borden 1973). Recovery of the community to pre-disturbance conditions is slow and alterations to community composition and species dominance can still be detected after thirty-five years (Estrada-Venegas 1995). Soil microarthropod populations in agricultural systems are known to be less diverse and less abundant because of intensive disruption of the soil or applications of biocides (Anderson 1988, Hendrix and Parmelee 1985, Wallwork 1970). Organic farming and no-tillage agricultural systems, in comparison to conventional tillage, which retains less surface organic matter, have been shown to increase numbers of microarthropods in agroecosystems (House *et al*. 1984, Usher 1985). Fertilizers have been shown to have little or no effect upon soil microarthropod populations in forest ecosystems (Huhta *et al*. 1967, Huhta *et al.* 1969, Marshall 1974). Compaction of soil because of harvesting or trampling reduces microarthropod densities (Usher1985, Vtorov 1993). Forest harvesting, like the other anthropogenic practices discussed above, directly and indirectly affects microarthropod communities.

The effects of 'intermediate' disturbances, such as the silvicultural practice of thinning, can be difficult to discern due to the resilience of organisms or stands, the histories of individual sites, or geologic, geographic and/or environmental heterogeneity that overwhelm management effects (Usher 1985, Bailey 1998, Madson 1997). To detect the effect of thinning upon soil microarthropod community composition, it is therefore necessary to establish strong indicators of the 'natural' heterogeneity and variability within the systems being measured.

The purpose of this section is to review soil microarthropod community patterns and factors influencing community composition at different spatial and temporal scales. Particular emphasis will be placed upon the oribatid mites (Acari: Oribatida).

Temporal patterns

Distributions of microarthropods fluctuate seasonally. Populations of microarthropods tend to reach a peak density during the late autumn/early winter months, with the lowest densities occurring during midsummer (Wallwork 1970, Fujikawa 1970a, Anderson 1988). This temporal pattern has been related to soil moisture and temperature: as spring transitions into summer, there is a shift from the wet season to the dry season, a decrease in soil moisture and an increase in soil temperature. In fall, the wet season begins again, increasing soil moisture and decreasing soil temperature (Cancela da Fonseca *et al*. 1995). In colder climes, a drop in temperature during the winter can also result in decreasing population densities (Asikidis and Stamou 1991), creating a second peak of population density during the spring as populations recover. Litterfall has also been identified as an environmental factor influencing the temporal distribution of microarthropods (Santos *et al*. 1978, Luxton 1981).

There have been few studies that follow long-term temporal distribution patterns in soil microarthropods. The disturbance studies (mentioned above) showed altered community patterns thirty-five years after the original disturbance. Chronosequence studies and studies of differing habitat-types have made the assumption that microarthropod populations follow the successional plant community through time (Fujikawa 1970a, Scheu and Schulz 1996).

Spatial patterns: Vertical

The vertical pattern of soil microarthropod distribution is also well established. Soil microarthropods tend to aggregate in the litter and the upper 0-5 cm of the soil (Wallwork 1970, Fujikawa 1970b, Usher 1976, Norton 1990). A few studies have shown seasonal migration of some species of mites from the litter layer into the mineral soil (Wallwork 1970, Norton 1990). Migrating mites tend to be medium or large-sized species. A few species of mites will even migrate on a daily basis out of the litter layer into the vegetation canopy (Wallwork 1970), though the reasons for this behavior are not well understood. Berthet (1964) found in a radioactive tagging study that oribatids move very short distances, with a maximum movement of five cm/day.

Spatial patterns: Horizontal

Soil microarthropods aggregate contagiously or in a clumped distribution horizontally within the soil (Aoki 1967, Fujikawa 1975a, Usher 1976, Schenker 1984, Norton 1990). The mechanisms thought to influence the clumped distribution pattern will be discussed under the heading ‘Factors influencing distributions’.

Usher (1976) analyzed the types of aggregation patterns occurring among soil microarthropod populations. He concluded from his analysis that Collembola and the Mesostigmata showed a Type I aggregation response. A Type I aggregation response is as the population density increases so does the number of aggregations per unit of surface area of volume. Oribatids showed a Type II aggregation response. A Type II aggregation response is as the population density increases so does the mean number of individuals per the aggregation. Thus, there is a relationship between population density and the number or size of aggregations that occur.

O’Connell and Bolger (1997) applied the Shorrocks ‘aggregation model’ of species coexistence to populations of fungivorous oribatids. Distribution patterns of adult oribatids were characterized by intraspecific aggregations. These results suggest that the aggregation patterns of adult oribatids facilitate the high diversity and numbers of microarthropods found in the soil. Juvenile oribatids showed interspecific aggregation patterns, indicating that juvenile aggregations were more resource-specific. This latter finding would account in part for juvenile distribution patterns observed by Usher (1976) and other researchers.

Hutchinson (1953, as cited by Usher 1976) describes five aggregations patterns. Vectorial aggregation is a distribution determined by external influences, e.g.

temperature, moisture, soil density. Reproductive aggregation is a distribution determined by the offspring remaining near the parents. Social aggregation is a distribution determined by signaling of various kinds, e.g. pheromones or chemical trails, which lead either to clumping or spacing. Coactive aggregation is a distribution determined by the interaction among species. Lastly, stochastic aggregation is a distribution determined by random forces. Usher (1976) suggests that the latter type of aggregation is the least likely to occur amongst soil microarthropods. He suggests instead that using Hutchinson's aggregation categories will aid in understanding the biological significance of the observed aggregations.

Abiotic factors influencing distributions

Several abiotic factors have been found to be important in determining distributions of soil microarthropod populations. One of the most important abiotic influences upon microarthropod populations is soil water content. Several studies have shown a positive correlation between soil moisture and the abundance of arthropods in soils (Wallwork 1970, Usher 1976, Vannier 1987, Whitford 1989, Asikidis and Stamou 1991). Closely related to soil moisture is soil temperature (Usher 1976, Whitford 1989, Asikidis and Stamou 1991, Cancela da Fonseca *et al*. 1995). Extreme temperatures have adverse effects upon soil microarthropods. A range of intermediate temperatures are preferred, which is species specific (Wallwork 1970).

Soil pH was found by Cancela da Fonseca *et al*. (1995) to be a greater influence upon microarthropod abundance than soil moisture or soil temperature. Soil pH was positively correlated with numbers of arthropods and negatively correlated with soil moisture and temperature. Klironomos and Kendrick (1995) also found pH to be one of five variables that structure microarthropod communities. Wallwork (1970) places less emphasis upon pH, merely indicating that the range of tolerance for soil acidity is species-specific.

Soil bulk density is negatively correlated with numbers of soil microarthropods (Wallwork 1970, Usher 1985). Lamoncha and Crossley (1998) found an increase in oribatid species diversity with increasing elevation. Natural disturbances, as mentioned in the introduction, eg. fires or floods, will alter microarthropod populations, most often disrupting and reducing community numbers.

Biotic factors influencing distributions

Soil organic matter is most commonly listed as the primary factor influencing microarthropod assemblages, increasing diversity and increasing the abundance of microarthropods (Fujikawa 1970b, Santos *et al*. 1978, Anderson 1988, Scheu and Schulz 1996). Soil organic matter was positively correlated with numbers of microarthropods.

Aggregations of microarthropods are postulated to often occur surrounding a food source (Usher 1976). Leonard and Anderson (1991) successfully demonstrated this relationship with laboratory studies. There have been few successful field demonstrations of this phenomenon, due to the patchiness of food resources and the lack of a high degree of preferential feeding by microarthropods in the field (Usher 1976). Klironomos and Kendrick (1995) published field results indicating not only an aggregation of microarthropods with food resources (fungal hyphae), but also a preference amongst soil microarthropods for darkly-pigmented fungi.

Location of other organisms is another factor influencing distributions of microarthropods. Schenker (1984) and Torgersen *et al*. (1995) both found a negative correlation between numbers of microarthropods and increasing distance from a single tree. Aoki (1967) found aggregations of mites along dead plant roots and fine root hairs (the rhizosphere). Cromack *et al*. (1988) found higher numbers of mites and Collembola in ectomycorrhizal fungal mats associated with Douglas-fir stands in western Oregon than in the surrounding mineral soil. Sgardelis (1988 as cited by Asikidis and Stamou, 1991) found increases in oribatid populations with the onset of microbial activity.

Usher (1976) found a general ‘sociability’ associated with aggregations of species. High numbers of arthropods would be aggregated with near zero environmental factors associated with the aggregation. Usher (1976) postulates that the animals are attracted to each other, either as prey items, as means of identifying an acceptable habitat, for reproductive purposes or for reasons as yet not understood.

Lastly, anthropogenic disturbances, primarily through management practices, influence microarthropod distributions. Several examples have already been discussed under the introduction. Grazed versus ungrazed lands are another set of management practices that affect microarthropods. Landscapes that are heavily grazed have lower numbers of microarthropods (Asikidis and Stamou 1991). Mowing has been found to occasionally increase microarthropod numbers (Christiansen *et al*. 1989).

Habitat Types: Macrohabitats

Microarthropods are distributed at the landscape scale over several different habitat types. Temperate forests are considered to contain the most diverse and abundant populations of microarthropods, with numbers as high as several hundred thousand per square meter (Wallwork 1970, Norton 1990). The high diversity and abundance are attributed to the large accumulation of soil organic matter, the complicated structure and multiple microhabitats that characterize forests (Aoki 1967, Fujikawa 1970a). Forest aggregations tend to be loosely distributed (Fujikawa 1975b).

Grasslands are less diverse than temperate forests, but with high abundance of microarthropods (Aoki 1967, Wallwork 1970, Anderson 1988). The habitat is characterized as less complex (Fujikawa 1975a) than forest habitats. Aggregations are small and compact (Fujikawa 1975b).

Microarthropod assemblages in deserts are strongly influenced by water availability. Rainfall and litterfall are the two determining factors of soil microarthropod community composition. Oribatids are abundant under shrubs, while Collembola are only found in the large playas (Santos *et al.* 1978). Whitford (1989) observed a diurnal pattern of microarthropod activity. The animals were most active near the surface during the coolest part of the day, 1 to 2 hours after sunrise. During the day, the animals would migrate vertically into the mineral soil, with activity occurring as deep as 20 cm.

Agricultural systems are characterized by low species diversity (Wallwork 1970, Anderson 1988). No-tillage and organic farming increase soil organic inputs into the system and increase microarthropod populations over those in conventional tillage (House *et al*. 1984, Usher 1985).

Habitat types: Microhabitats

Microarthropods can be found in the majority, if not all, the microhabitats within a forested or agricultural ecosystem. Aoki (1967) did a survey of microhabitats within a 10 x 10 m forest plot and identified fourteen microhabitats. These included mosses, fungus, bark, fallen twigs, fresh fallen leaves of various species, coarse woody debris, plant reproductive structures, the humus layer, the mineral soil and the rhizosphere, including fine, dead roots. Asikidis and Stamou (1991) found that larger, hard-skeleton, macrophagous mites were more likely to be associated with the drier microhabitats, such as mosses, lichens, and grasses. Small-sized, soft-exoskeleton, hygrophilious, microphytophages were more likely to be associated with cooler, moister microhabitats.

Summary

Soil microarthropods are extremely diverse and abundant. The community composition of an assemblage of microarthropods in any given ecosystem is very complex. Seasonal, vertical and horizontal distribution patterns work synergistically to create a microarthropod assemblage. Microarthropods are positively correlated with soil moisture, soil temperature and soil organic matter. Populations are negatively correlated with high soil density and with distance from the nearest tree. Microarthropods are positively correlated with other soil organisms, including microbes, fungi, plants and other microarthropods.

Management has been demonstrated to alter microarthropod communities through reduction of species diversity or abundance. Many interactions and effects are difficult to quantify or unknown due to a lack of information on the biology of species within the ecosystem. Observations of species taken at the scale of the microhabitat have been moderately successful in gaining insight into species interactions and system processes. To evaluate the effect of an ‘intermediate’ disturbance upon the landscape, such as the silvicultural practice of thinning, the microhabitat is an appropriate scale to measure.

Silvicultural practices

Silviculture is the cultivation of forest trees and most silvicultural methods are applied to forest harvesting, though all can be adapted for purposes of managing other forest attributes such as wildlife habitat, species diversity, small forest products, and forest structure. Since this study examines the response of biotic communities and abiotic factors to one form of silvicultural management, two-age regeneration, a brief review of the more common silvicultural methods in use today in North American forests is provided below to assist the non-silviculturist in placing the two-age method relative to other types of silvicultural practices.

Clear-cutting

Clear-cutting is the practice of removing the entire stand biomass at the same time, followed by natural or artificial regeneration (Loftis 1989, Smith *et al*. 1997). This creates even-aged stands that can extend over substantial areas. It is regarded in the short-term as being more economically feasible than alternative methods that require more careful selection and preparation before, during, and post harvest, yet do not yield as great of economic return in the short-term (Smith 1995, Matthew 1989). For this reason, it has been the prevalent method of forest harvesting in the United States. It is important to take stand species composition and site factors into consideration before clear-cutting as individual tree species each respond differently to clear-cutting. Some species require replanting to regenerate, others need to have reached a stage of advanced regeneration before harvesting to successfully regenerate, while a third group can regenerate successfully as stump and root sprouts, also known as coppice systems (Loftis 1989). Hardwood stands in the southern Appalachians respond favorably to clear-cutting, with clear-cut stands rapidly recovering leaf area and net primary production (Boring and Swank 1986) and biomass (Smith 1995). Species diversity of the vegetation is also higher in the initial stages of stand development post-harvest (Elliott and Swank 1994). Clear-cutting has been shown to initially increase soil moisture one year post-harvest and then decrease soil moisture in subsequent years (Gray *et al*. 2002, Griffiths and Swanson 2001, Marra and Edmonds 1998, Reynolds *et al*. 2000). Soil temperature is higher in harvested stands and more variable (Ballard 2000, Griffiths and Swanson 2001, Reynolds *et al*. 2000, Seastedt and Crossley 1981, Swank and Vose 1988). Litter depth, percent soil organic matter, and percent ectomycorrhizal mat cover decrease in clear-cut stands (Griffiths and Swanson 2001).

Thinning

Thinning is the silvicultural practice of reducing stand density for the purpose of increasing the availability of stand resources to remaining trees, increasing tree growth of remaining trees, decreasing or eliminating the presence of undesirable species, maintaining stands in productive condition, and generating income without waiting for the full stand rotation. (Beck 1989, Smith *et al*. 1997). Thinning can be done in the understory cohort or amongst the overstory, or crown cohort, to produce different effects. Understory thinning, also known as low thinning, mimics natural mortality that occurs as a result of self-thinning in the normal development of even-aged stands. Overstory, or crown thinning, removes trees from the canopy to favor understory species or release advance regeneration. Another form of thinning is removal of dominant individuals, also known as high-grading. If not used carefully, this method can remove desirable species and individuals to the overall detriment of the stand in the long-term (Smith *et al*. 1997).

Thinning can decrease threat of disease and insects as the trees experience less stress than when overstocked (Smith 1995), but it requires more intensive management over short-periods of time.

Regeneration methods

There are several types of regeneration methods, which are also known as selection harvests. Selection methods have become more widespread in the last decade as public agencies have shifted away from clear-cutting as the predominant silvicultural practice (Caza 1993, Franklin 1993, Hopwood 1991, McComb *et al*. 1993). Two-age regeneration is an uneven selection method that removes approximately two-thirds of the stand basal area, releasing the advance regeneration cohort, while retaining mature trees as refugia for fauna and as a source of seed and genetic variation within the stand (Smith *et al*. 1997). This method also releases shade-intolerant species while being more aesthetically pleasing than clear-cuts (Miller *et al*. 1995), which is especially important in areas where tourism and recreation from national forests are an integral part of the local economy. Two-age regeneration increases vegetation diversity within the stand and also reduces the effect of insect outbreaks and disease compared to even-aged stands (Miller *et al*. 1995).

Irregular shelterwood regeneration is similar to two-age regeneration in creating an uneven-aged stand, retaining seed trees as habitat and refugia, and in releasing cohorts of advance regeneration. It is distinguished from two-age regeneration by a greater number of age-classes within the stand and a shorter period between regeneration harvests. A greater basal area is also usually retained within the stand (Matthews 1989).

Group selection is another regeneration practice for creating uneven aged stands. Groups of trees within small areas of the stand are harvested to create a patchy mosaic of "mini-clearcuts" within the stand. Typical openings range from 0.08-0.20 ha (Johnson *et al*. 2002). Size of the clearing can be varied to accommodate the regeneration requirements of different species or to create diverse habitat patches for wildlife (Smith *et al*. 1997). It also has the advantage of being cheaper to harvest than shelterwood or two-age cuts, with less damage done to residual trees.

Forest harvesting and soil microarthropods

Studies examining the effects of forest harvesting on soil microarthropod communities are rare. A generous estimation of the number of studies completed in the last century that examine this topic would be less than 30, and is, perhaps more accurately, closer to 20. Before the early seventies, the handful of studies performed were European, with the majority unpublished in the English language. Excepting the earliest English publications on this topic, these European studies are not cited and largely ignored. Thus, the literature on this topic in the English language is generally considered to begin with the comprehensive study conducted by Huhta *et al*. (1967).

Huhta *et al*. (1967) examined the effect of silvicultural practices of clear-cutting, thinning, burning, fertilizing, and pesticide application on soil microarthropod communities in coniferous forests in Finland. They found that oribatids respond to clear-cutting with an initial increase in population density in the first year, followed by a gradual decrease in numbers that is significantly less by the fourth year. Community recovery is slow and a follow-up study (Huhta *et al*. 1969) found no increase in population seven years after harvesting. Thinning had a milder effect on oribatid communities, but followed a similar trend (Huhta *et al*. 1967). Huhta *et al*. (1967) speculated that the decrease in oribatid communities was due to a reduction in organic matter, which serves as the substrate for their main food resource, fungi.

Collembola populations had a response opposite to that of the oribatid communities, with a slow increase in population as a result of clear-cutting (Huhta *et al*. 1967). The reverse was true in the thinned stands, which saw a decrease in Collembolan populations. This decrease was attributed to the effect of thinning on microclimatic conditions. In the follow-up study (Huhta *et al*. 1969), Collembola populations had markedly increased and were approaching pre-cut levels. The reason for this is unknown, but was speculated to be in part due to the rapid reproductive rates of Collembola (Huhta *et al*. 1969).

Later studies examining the effect of clear-cutting on soil microarthropods found similar decreases in microarthropod densities following clear-cutting (Abbott *et al*. 1980, Bird and Chatarpaul 1986, Blair and Crossley 1988, Huhta 1976, Marra and Edmonds 1998, Seastedt and Crossley 1981, Vlug and Borden 1973). However, only Huhta (1976) also reported an initial increase in oribatid density in the first year after harvest. The other studies only saw decreases in microarthropod populations after clear-cutting. Population decreases were attributed to many factors including decreased food resources (Huhta 1976), erosion (Marra and Edmonds 1988), high temperatures (Abbott *et al*. 1980), vertical distribution and amount of organic matter (Seastedt and Crossley 1981), decreased food supply, low moisture, high temperatures and compaction (Bird and Chatarpaul 1986), and high temperatures and high pH (Vlug and Borden 1973).

Interestingly, despite decreased densities, the taxa present usually remained the same, with shifts in species dominance occurring (Bird and Chatarpaul 1986, Huhta *et al*. 1967, Seastedt and Crossley 1981). Bird *et al*. (2000), in a study similar to Bird and Chatarpaul (1986), studied the differences between hand-felled, bole only harvesting, referred to as conventional harvesting by Bird and Chatarpaul (1986), and whole-tree harvesting. Both studies found lower densities of microarthropods in the whole-tree harvested stand, which was harvested more intensively.

The effects of forest harvesting methods other than clearcutting, such as thinning, and regeneration treatments, on microarthropods have received even less attention. The effects of thinning on microarthropod populations have been examined in only a few studies, including the results of Huhta *et al*. (1967) mentioned above. Thinning is the silvicultural practice of reducing stand density through partial removal of the overstory canopy (Bailey and Tappeiner 1998). All studies showed a decrease of microarthropod densities in thinned stands (Huhta *et al*. 1967, Hoekstra *et al*. 1995, Madson 1997). Madson (1997) found that litter-dwelling microarthropods were more responsive to stand treatments than mineral soil-dwelling microarthropods. Huhta *et al*. (1967) similarly mentioned that characteristic patterns of fluctuation by individual taxa tended to mask the effect of silvicultural practices.

Only one study has examined the effects of regeneration treatments, such as green-tree retention, shelterwood cuts, and group selection, on soil microarthropods (Siira-Pietikäinen *et al*. 2001). Collembola densities did not change during the 3-year study, until the last sample, which saw a slight decrease in Collembola densities in the harvested sites. It was concluded that Collembola population fluctuations are linked to habitat type and microclimate (Siira-Pietikäinen *et al*. 2001). Oribatids were not sampled.

Conclusions

In summary, forest harvesting negatively affects soil microarthropod densities. Intensity of harvest can vary this effect, with more intensive harvest methods causing a greater decrease in abundance. Alternative forest harvesting methods, such as thinning and regeneration methods, appear to have a lesser effect upon soil microarthropods than does clear-cutting. It is rare that taxa disappear completely from a harvested site, but species dominance often shifts, with formerly rare species becoming more abundant. O'Connell and Bolger's (1988) adaptation of the probabilistic niche hypothesis to soil arthropod community diversity may in part explain this switch in the abundance of certain taxa within the community. Organic matter abundance and distribution, moisture, and temperature are all generally agreed to be the driving factors behind soil microarthropod community abundance and distribution. Observations of species taken at the scale of the microhabitat and microclimate have been moderately successful in gaining insight into species interactions and system processes (Anderson 1988, Aoki 1967, Asikidis and Stamou 1991, Hansen, 2000, Marra and Edmonds 1998, Siira-Pietikäinen *et al*. 2001). Ironically, Setälä *et al*. (2000) recently found that changes occurring at the species level of soil fauna as a result of harvesting have little effect upon stand productivity. If harvesting methods leave the soil organic layer relatively intact, then soil biota are buffered against drastic changes in their environment and the processes they contribute to continue (Setälä *et al*. 2000). High redundancy of taxa within functional groups also probably contributes to the scant effect of lowered densities of soil microarthropods upon stand productivity.

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CHAPTER 3

EFFECT OF TWO-AGE REGENERATION ON MICROCLIMATIC CONDITIONS WITHIN MIXED NORTHERN RED OAK (*QUERCUS RUBRA*) STANDS IN THE SOUTHERN APPALACHIANS[1]

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Abstract

Soil microclimatic conditions within a forest stand have been shown to determine the parameters for successful establishment of seedlings, the decomposition rate of organic matter, or the composition of soil fauna communities. Changes in soil temperature and soil moisture have been shown to alter the abundance and distribution of organisms within the soil. We assessed the soil microclimatic conditions between two-age regeneration and control stands and within microhabitats established by two-age regeneration treatments at Wine Spring Creek, North Carolina. Two-age cut stands had significantly greater fluctuations in soil temperatures, higher soil temperatures in summer, cooler soil temperatures in winter, decreased litter depth, and a trend towards decreased soil water content compared to nearby uncut stands. The greatest fluctuation in temperature was in the coppice shrub microhabitat. Skid roads had the greatest bulk density and the least amount of moisture. The woody debris habitat accumulated the greatest amount of litter. Examining spatial patterns of microhabitat distribution and frequency across harvested stands may be a useful tool for elucidating treatment effects.

Keywords: two-age regeneration, microclimate, forest harvesting, hardwood forests, southern Appalachians, soil water content, soil temperature, bulk density, microhabitats, leaf litter

Introduction

Variation in microclimatic conditions in forest stands can have long-term effects on stand structure and growth. Changes in soil moisture, soil temperature, or organic matter quality and quantity can affect seedling establishment and growth (Gray and Spies 1997, Zabowski *et al*. 2000), litter decomposition rates (Prescott *et al*. 2000), nutrient cycling (Ballard 2000, Gobran *et al*. 1998), and community composition of soil organisms (Hansen and Coleman 1998, Seastedt and Crossley 1981, Whitford 1989).

Forest harvesting is a landscape-level disturbance that alters microclimatic conditions in a patchy mosaic across stands. Clear-cutting and gap formation in coniferous forests has been shown to initially increase soil moisture one year post-harvest and then decrease soil moisture in subsequent years (Gray *et al*. 2002, Griffiths and Swanson 2001, Marra and Edmonds 1998, Reynolds *et al*. 2000). Soil temperature is higher in harvested stands and more variable (Ballard 2000, Griffiths and Swanson 2001, Reynolds *et al*. 2000, Swank and Vose 1988). Litter depth, percent soil organic matter, and percent ectomycorrhizal mat cover decrease in clear-cut stands (Griffiths and Swanson 2001).

Management of forest lands by federal agencies has shifted in recent years away from clear-cutting towards an increase in selective harvest and regeneration methods. The effect of these methods on microclimatic conditions is only beginning to be examined in a wide variety of forest ecosystems. The goal of this study was to characterize the effect of two-age regeneration on microclimatic conditions within hardwood stands in the southern Appalachians. This study was part of a larger study examining the response of soil microarthropod communities to two-age regeneration and was conducted to identify abiotic factors influencing soil microarthropod community dynamics. Our objectives were to (*i*) compare landscape changes in microclimatic conditions between two-age regeneration stands and controls, and (*ii*) compare local changes in microclimatic conditions among microhabitats created by the harvesting process. We hypothesized that two-age regeneration methods will increase soil temperature, will decrease soil water content, and decrease litter depth in forested stands. We hypothesized that the skid road microhabitat will have the greatest bulk density from compaction caused by skidding, the warmest soil temperatures since it has no canopy cover, and show the greatest variation in soil temperatures since it is the most exposed. We hypothesized that the mature tree and coppice/shrub microhabitats will have the lowest bulk density since harvesting operations would have been less concentrated near residual trees and shrubs, cooler soil temperatures due to the intact canopy cover, will exhibit the least variation in soil temperature for the same reason, and the greatest accumulation of litter. We hypothesized that the coarse woody debris microhabitat will have the highest soil water content since there will be little moisture uptake by vegetation in that microhabitat.

Material and Methods

Site Description

The study was conducted at Wine Spring Creek Watershed (latitude: 83°35’43” W, longitude: 35°10’36” N) in the Nantahala National Forest, Wayah Ranger District, North Carolina, approximately one hour’s drive (60 km) northwest of the Coweeta Hydrologic Laboratory in Otto, NC. The 1820 ha basin is a demonstration project of ecosystem management, initiated in the early 1990’s, that provides an integrated, interdisciplinary ecosystem approach to planning, research, and management. Eleven sites were selected by ground surveys conducted by USFS employees in northern red oak-flame azalea (*Quercus rubra-Rhododendron calendulaceum*) dominated communities on northwest facing slopes.

McNab and Browning (1993) classified these ridges as dry, high-elevation, with moderate to steep slopes. Mean monthly temperature ranges from 3^{o}C in January to 22^{o}C in July. Precipitation averages 1737 mm annually and is evenly distributed throughout the growing season, with only a little falling as snow. Growing season is 180 days. The average temperature is lower, growing season shorter, and wind speeds higher at these sites relative to lower elevations in the watershed. Soil parent material consists of a metamorphic formation of biotite gneiss, biotite, garnet gneiss, and amphibolite. Soils are mapped as Wayah series and the A horizon is classified as black sandy-loam, with 18% organic matter (Soil Survey Division 2001).

The study sites ranged in elevation from 1,380-1,580 m and were 4.0-6.6 ha in size. The Forest Service acquired the watershed in 1912 after it had been logged over. The stands selected for this study were mature, between 70-80 years old, with minimal disturbance since acquisition by the Forest Service (W. J. Culpepper, personal communication). For a full site description, see Elliott and Hewitt (1997) and McNab and Browning (1993).

A silviculturist with the Wayah District office assigned each site to one of three regeneration treatments (two-age cut, shelterwood, group selection), with three replicates each, or to the control (uncut), with two replicates. Criteria used to assign treatment type included species composition, geographic location, and proximity to roads (W. J. Culpepper, personal communication). This study was performed in the two-age cuts (sites 5, 9, 10) and control sites (sites 6, 7). The regeneration treatments were logged in the summer of 1997. The stands were contract sold to a local timber company and harvested using a skidder unit. The skid roads were bladed with a bull-dozer and reseeded after harvesting was completed. In November of 1997, the stands were site prepared for natural regeneration by chainsaw felling of undesirable or damaged residual stems. After harvesting and site preparation, 90% of the vegetation in the two-age stands had been removed. The two-age regeneration cuts had a 3.67 m^2 residual basal area per hectare (W. J. Culpepper, personal communication).

Microhabitats

The harvested stands were characterized by distinct microhabitats created by the regeneration treatment. The first microhabitat consisted of remaining mature trees (MT) scattered throughout the stand, representing approximately 30% of the original stand basal area. The second microhabitat consisted of coppices from the harvested trees and shrubs, which were predominantly flame azalea (CS). Due to a low chip mill market at the time of harvest, boles were stripped of the crown and branches on site and the slash left behind. Large piles of coarse woody debris (WD), reaching sizes of two meters in height and three meters in diameter, were found throughout the stand. Clearings within the stand were characterized by herbaceous growth (HG), including grass, ferns, and other perennial herbaceous plants. Lastly, the skid roads (SR) used for harvesting the stand covered approximately 5% of the stand.

Abiotic measures

Soil temperature was measured using Onset Corporation Hobo data loggers at five points within each stand (n=5/stand, n=25/date). The five points were stratified to represent each microhabitat type within the harvested stands. To prevent exposure to moisture, the data loggers were placed within 7.5-cm diameter and 2.0-cm depth candy tins (La Vosgienne), rice was added to eliminate the surrounding air layer within the tin, and the tins were sealed with Vaseline and electrical tape. The tins were then placed within the O and A horizons, 2-4 cm below the top of the forest floor, including the litter layer. Temperature accuracy of the data loggers has been measured as within 0.5-1^{o}C at temperatures between -20-60^{o}C (Onset Computer Corporation 1997). Soil temperature was measured daily every two and a half-hours in degrees Celsius for the periods between November-December 1998, February-July 1999, and June-November 2000.

Soil water content was measured using the gravimetric method. Cores, measuring 4.5-cm diameter and 5.0-cm depth, were taken at fifteen points randomly selected within each stand (n=15/stand, n=75/date). For each core, the litter layer was removed and the top five cm of the mineral layer, including the Al horizon or well-decomposed organic material, was sampled. In the harvested stands, the points were stratified to represent all five microhabitat types (n=3/microhabitat). Soil water content was measured in April 1999, May 1999, and July 1999. Cores were dried for one week at 65^{o}C in a mechanical convection oven. Soil water content was calculated by dividing the water weight by the soil dry weight. Bulk density of the soil was calculated using the same core samples. Bulk density was calculated by dividing the oven dry weight by the volume of the core.

Litter layer depth was measured at nine locations at equal distances apart within 0.09 m^2 and averaged. The litter layer was defined as the non-fragmented or partially fragmented leaf and organic material above the H, or O, horizons. Litter depth was measured at the same time and place as the moisture cores (n=15/stand, n=75 date) and on five other dates in spring and fall (May 1998, November 1998, May 1999, November 1999, June 2000) in a related study (n=50/stand, n=250/date).

Air temperature and precipitation were collected at a climate station within the Wine Spring Ecosystem Management Area near Forest Service Road 711 and maintained by the Coweeta Hydrologic Laboratory. Air temperature was measured hourly in degrees Celsius with a Vaisala HMP45C unit from Campbell Scientific. The precipitation was measured in inches with a Belfort universal recording rain gauge, corrected for evaporation with a Belfort non-recording precipitation gauge to obtain the total daily precipitation. The data was later converted to millimeters.

Statistical Analysis

Exploratory data analysis of the soil water content, bulk density, and litter depth data showed the data to follow non-normal distributions, with a long-tail on the right hand side. Soil water content and bulk density were transformed before statistical analysis with a log10 transformation and litter depth was transformed using a square root transformation. Soil temperature was analyzed without transformation.

Average monthly soil temperature, soil water content, bulk density, and litter depth collected in April, May and July 1999 were analyzed with repeated measures ANOVA using the general linear model procedure (GLM) in SAS 8.2 (SAS Institute, Inc. 2001). Litter depth for the spring and fall sample dates was analyzed with a nested ANOVA using the GLM procedure in SAS 8.2. Coefficients of variation for daily soil temperature were calculated using the average and standard deviation of all measured dates and analyzed with a one-way ANOVA in S-Plus 6.0.

Results

Ambient conditions

Average daily air temperature for each month was similar across all years of the study period (Fig. 3.1a). The maximum average daily air temperature was 20°C in the summer months and the minimum average daily air temperature was -1°C in the winter months. Annual precipitation was highest in 1997 (188 cm), followed closely by 1998 (182 cm) (Fig. 3.1b). 1999 and 2000 were increasingly drier, with an annual precipitation of 153 cm in 1999 and 138 cm in 2000. Precipitation in 1999 was extremely variable across the year, with daily average precipitation in the summer months reaching the same amount as in previous years.

Treatment effects

Average daily soil temperature was warmer in the two-age stands in the spring months and warmer in the control stands in the fall and winter months (p=0.0169) (Fig. 3.2a). Variation in daily soil temperature was also significantly higher in the two-age stands (p=0.00006) (Fig. 3.2b), with the greatest fluctuation in daily temperatures occurring in the winter months. Summers showed the least variation in daily soil temperature in both the control and two-age stands.

Average gravimetric soil water content was high in all stands and was not significantly different between treatments (Fig. 3.3a). There was a trend towards higher moisture content in the control sites. Soil bulk density was also not significantly different between treatments (Fig. 3.3b).

Average litter depth measured in April, May, and July of 1999 was significantly deeper in control stands (p-value = 0.0193) (Fig. 3.3c). Average litter depth measured during the spring and fall microarthropod sampling dates of the study period was also significantly deeper (p-value < 0.0001) (Fig. 3.4) in the control stands.

Microhabitat effects

Average daily soil temperature was not significantly different among microhabitats (Figs. 3.5a-c, 3.6a-b), but tended to be 1-2°C higher on skid roads in spring and summer months. Variation in daily soil temperature was significantly different among microhabitats (p=0.0347) (Figs. 3.5d-f, 3.6c-d), with the greatest fluctuation in daily temperatures usually occurring in the winter months in the coppice/shrub microhabitat. The least fluctuation in daily temperature usually occurred in the skid road microhabitat. Summers showed the least variation in daily soil temperature in all microhabitat types.

Average gravimetric soil water content was low in all microhabitat types and was not significantly different among microhabitats (Fig. 3.7a). There was a trend towards lower moisture content in the skid road microhabitats. Soil bulk density was significantly different among microhabitats (p-value < 0.0001) (Fig. 3.7b), but this was due entirely to the significantly higher bulk density found in the skid road microhabitat.

Average litter depth measured in April, May, and July of 1999 was significantly different among microhabitats (p-value < 0.0001), with the lowest amount of litter found in the skid road habitats (Fig. 3.7c). Litter depth within the herbaceous microhabitat was also significantly less than that in the three remaining microhabitats. Average litter depth measured during the spring and fall sample dates of the study period was also significantly different (p-value < 0.0001) (Fig. 3.8) among microhabitats and followed a similar pattern during the first two-years post-harvest. The depth of the litter layer in the herbaceous microhabitat had increased to that of the other microhabitats in November 1999 and June 2000, while the litter layer in the skid roads remained low. The coarse woody debris habitat tended to have the highest amount of litter through time.

Stand effects

Average daily soil temperature was significantly different among the three two-age stands (p-value = 0.0192) and between the two control stands (p-value < 0.0001) (Figs. 3.9a-c, 3.10a-b), with higher average daily soil temperature per month consistently found in site 10 of the two-age stands and site 7 of the control stands. Variation in daily soil temperature was not significantly different between stands of either type (Figs. 3.9d-f, 3.10c-d), but there was a trend towards less variation in temperature in site 10 and site 7.

Average gravimetric soil water content was significantly different among the three two-age stands and between the two control stands (Fig. 3.11a). Soil water content was higher in control site 6 and in two-age site 10. Two-age site 5 usually had the lowest soil water content. Soil bulk density was significantly different between the control stands (p-value = 0.0007) (Fig. 3.11b), but not among the two-age regeneration stands. Site 6 had a higher bulk density than site 7. Among the two-age stands, there was a trend towards a higher bulk density in site 5 and a lower bulk density in site 10.

Average litter depth measured in April, May, and July of 1999 was significantly different between the control stands (p-value < 0.0001), but was not significantly different among the two-age regeneration stands (Fig. 3.11c). Site 7 had significantly deeper litter than the other control stand. Among the two-age stands, there was a trend towards a deeper litter layer at site 5. In contrast, average litter depth measured during the spring and fall sample dates of the study period was significantly different (p-value = 0.0011) (Fig. 3.12) among two-age regeneration stands. Site 5 had a significantly deeper litter layer, which is consistent with the trend seen in the three-month data. Control site 6 had a deeper litter layer in the first year post-harvest, but in the next two years, the deeper litter layer was in site 7.

Discussion

Two-age regeneration alters microclimatic conditions across the landscape towards significantly greater fluctuations in soil temperatures, higher soil temperatures in summer months, cooler soil temperatures in winter months, decreased litter depth, and a trend towards decreased soil water content. These results are consistent with earlier studies conducted in coniferous forests and clear-cut stands (Ballard 2000, Gray *et al*. 2002, Griffiths and Swanson 2001, Marra and Edmonds 1998).

Soil temperatures at local scales within microhabitats created or exacerbated by the harvesting process were not significantly different, but varied significantly in the degree of fluctuation in daily temperature. Soil water content and bulk density were not significantly different among microhabitats. Litter depth varied significantly among microhabitats, suggesting litter depth was a primary driver of differences in the community composition of soil organisms among microhabitats (Madson 2003). The relatively rapid and high accumulation of litter and organic material in the woody debris microhabitat provided a protected food resource and a stable, complex habitat at small scales for soil microarthropods, arthropods, salamanders and small mammals to use. This result compliments the findings of other studies that retention of slash and harvesting residues on site is important for retaining nutrients on site, allowing the gradual accumulation of organic matter, and for providing large-scale habitat structure and complexity within a stand (Lanham and Guynn, Jr. 1996, Mattson *et al*. 1987, Schowalter *et al*. 1998, Whiles and Grubaugh 1996).

Significant differences in soil temperature, soil water content, bulk density, and litter depth among stands of the same treatment suggest a strong site specific influence on abiotic conditions. Site specific influences in this case were overwhelmed by treatment effects, but were stronger overall than localized effects of microhabitats created by the harvesting process. Abiotic conditions were most likely altered between sites due to local variations in topography, location relative to first-order streams and springs, wind speed, percent leaf area cover, and edge orientations (Chen *et al*. 1995).

The effect of two-age regeneration on abiotic conditions such as soil temperature, soil water content, and organic matter accumulation across the landscape implies the potential for corresponding changes in decomposition rates, microbial communities, rates of nutrient cycling, seedling germination, and vegetation. Studies examining the effects of harvesting on these variables found increases in net nitrogen-mineralization in harvested stands (Griffiths and Swanson 2001, Reynolds *et al*. 2000), lower decomposition rates in clear-cut stands (Abbott and Crossley 1982, Blair and Crossley 1988), and shifts in the bacterial communities and decreases in the densities of nitrogen fixers and ectomycorrhizal fungi (Griffiths and Swanson 2001, Marshall 2000). Yet studies of chronosequences of clear-cut and selectively harvested stands have found that recovery of ecosystem function and diversity within these stands is possible even over relatively short periods of time (30-50 years), depending on management goals (Bailey *et* *al*. 1998, Elliott *et al*. 2002, Franklin *et al*. 2002, Griffiths and Swanson 2001, Marshall 2000).

North American forests have evolved through time to be resistant to chronic, even catastrophic, disturbances (Franklin *et al*. 2002, Seymour *et al*. 2002). Combining multiple silvicultural practices to create a mosaic of habitats, age-classes, and structures, without excess in any one practice, will allow forest managers to maintain ecosystem processes, maximum biological diversity, and to maximize public use of forest lands.

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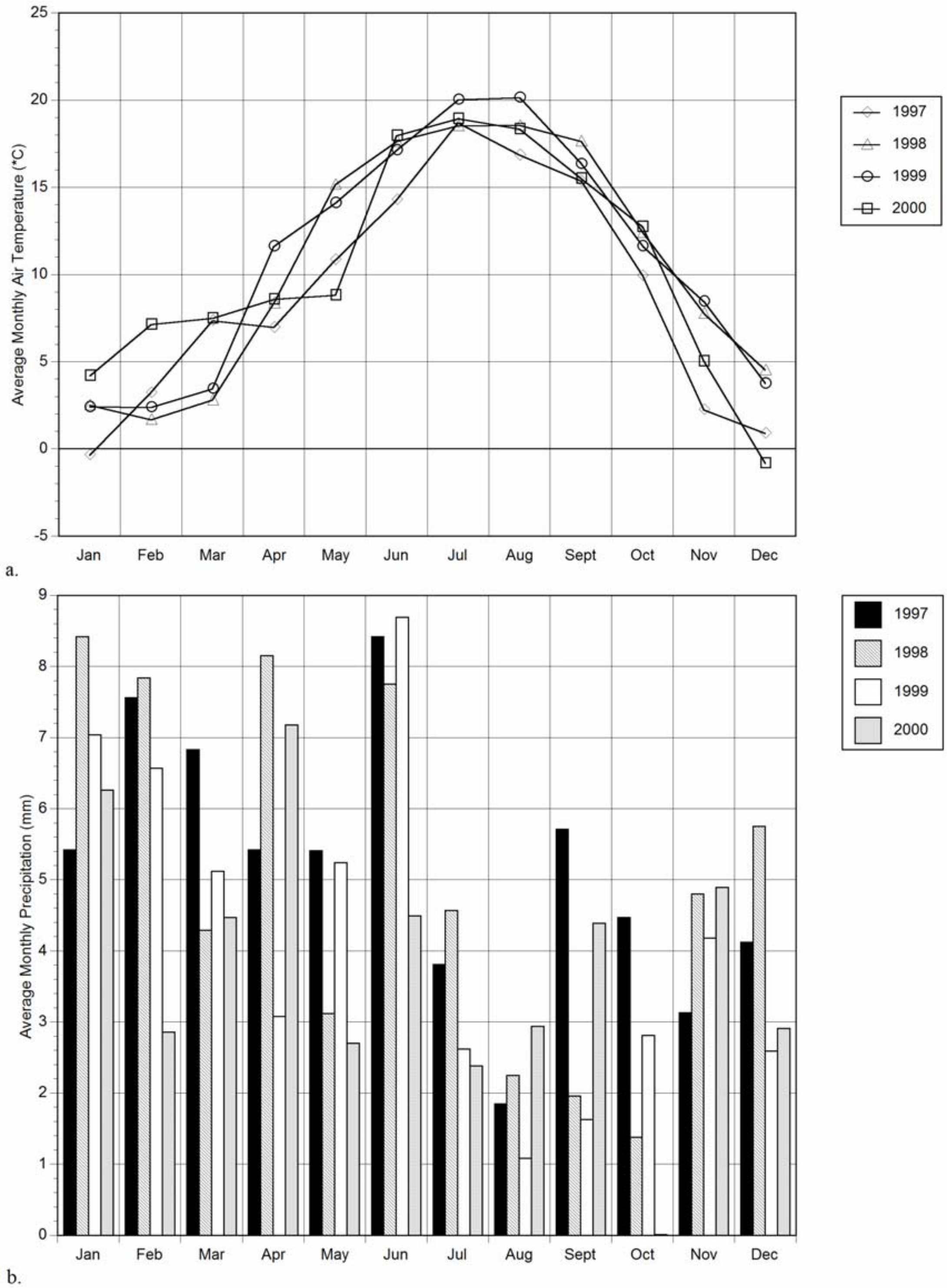

Figure 3.1. a) Average monthly air temperature (^{o}C) measured at Wine Spring Creek watershed, N.C. 1997-2000; b) average monthly precipitation (mm) measured at Wine Spring Creek watershed, N.C., 1997-2000.

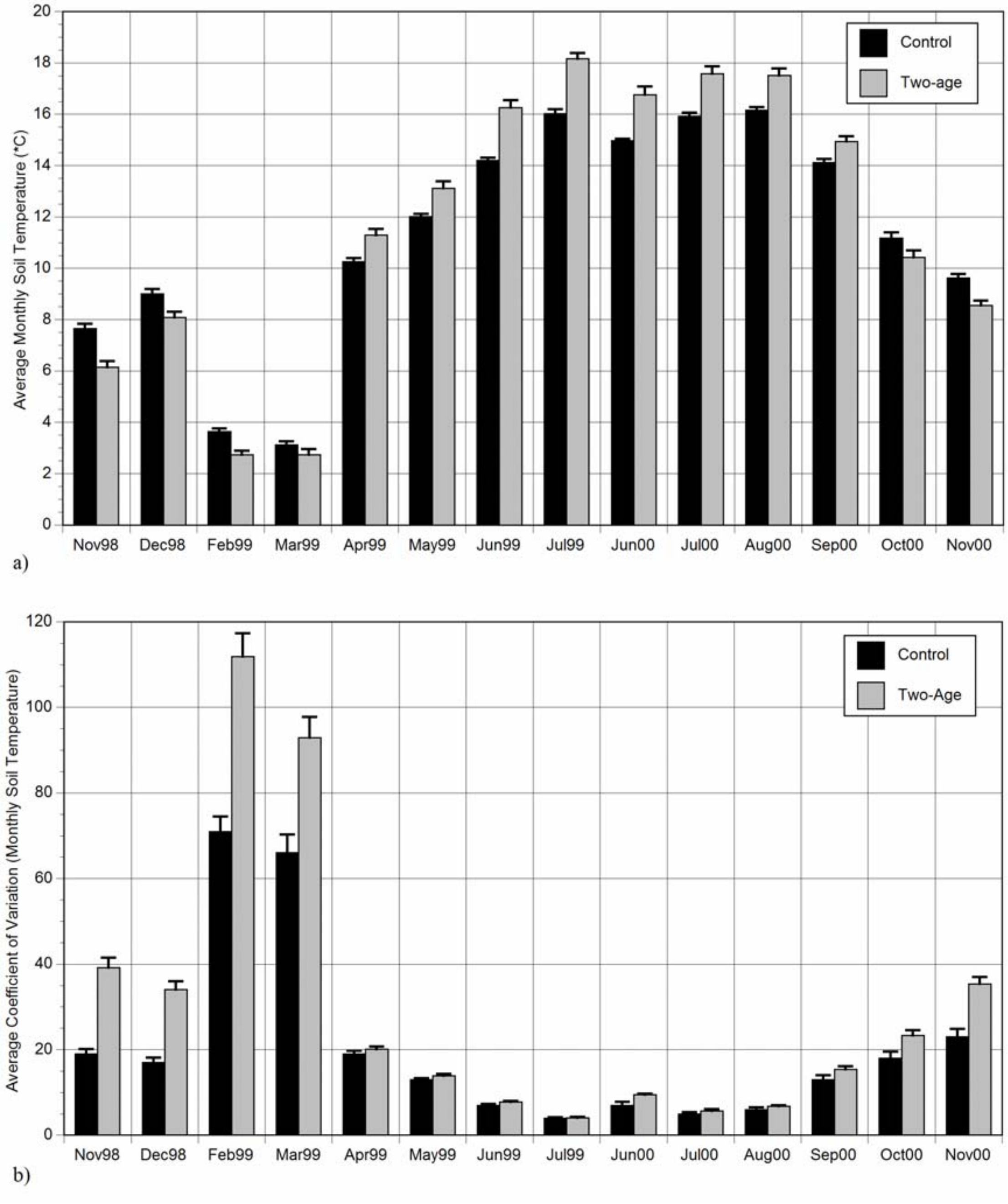

Figure. 3.2. a) Average monthly soil temperature (control n=10 data loggers, 300 measurements/month/data logger, two-age n=15 data loggers, 450 measurements/month/data logger) and b) the average coefficient of variation for monthly soil temperature recorded within control and two-age regeneration (n= hardwood stands at Wine Spring Creek watershed, N.C.

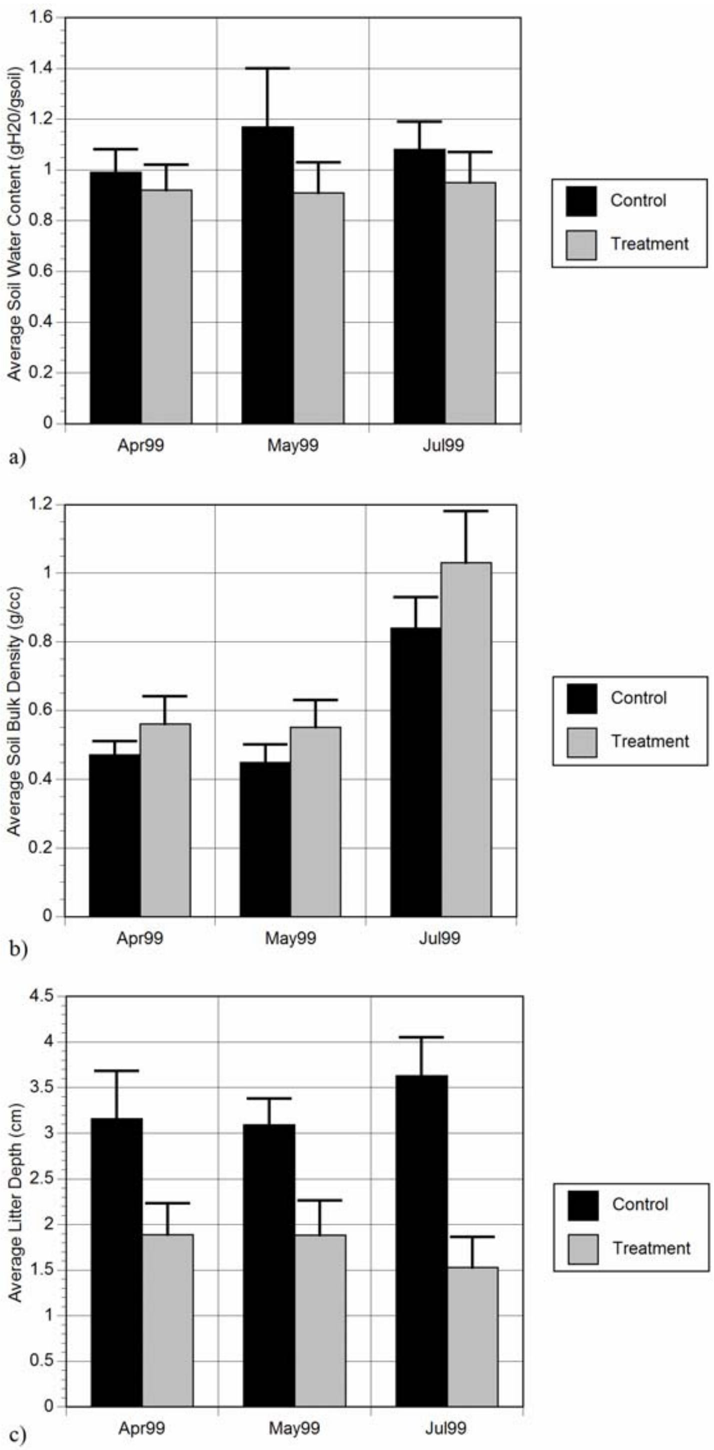

Figure 3.3. a) Average gravimetric soil water content, b) bulk density, and c) litter depth for April, May and July 1999 between regeneration (n=45) and control (n=30) treatments at Wine Spring Creek watershed, N.C.

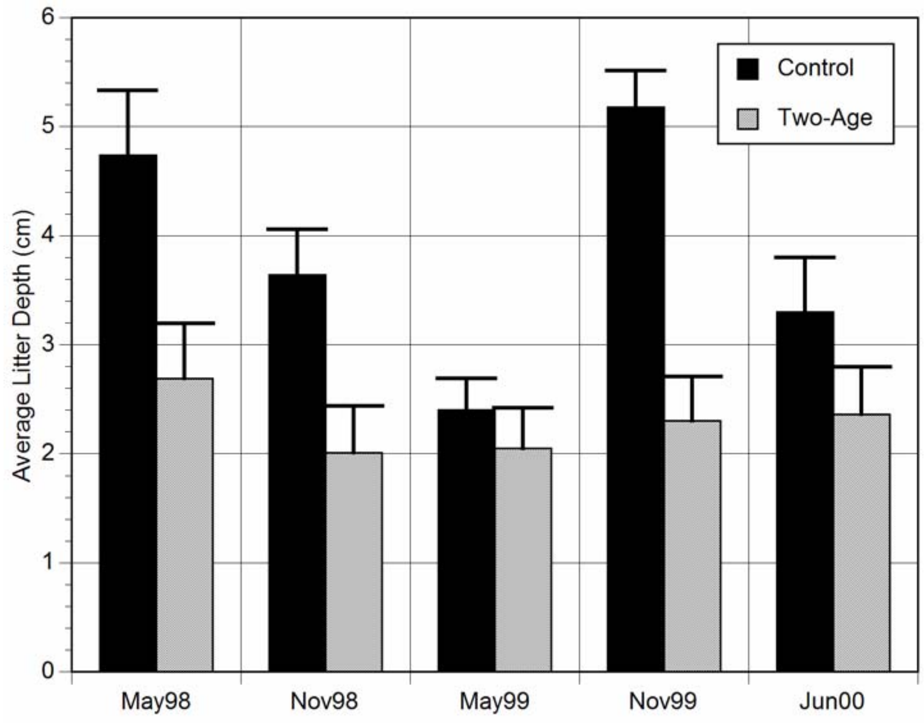

Figure 3.4. Average litter depth (cm) during the spring and fall microarthropod sample dates (n=250/date) at Wine Spring Creek watershed, N.C.

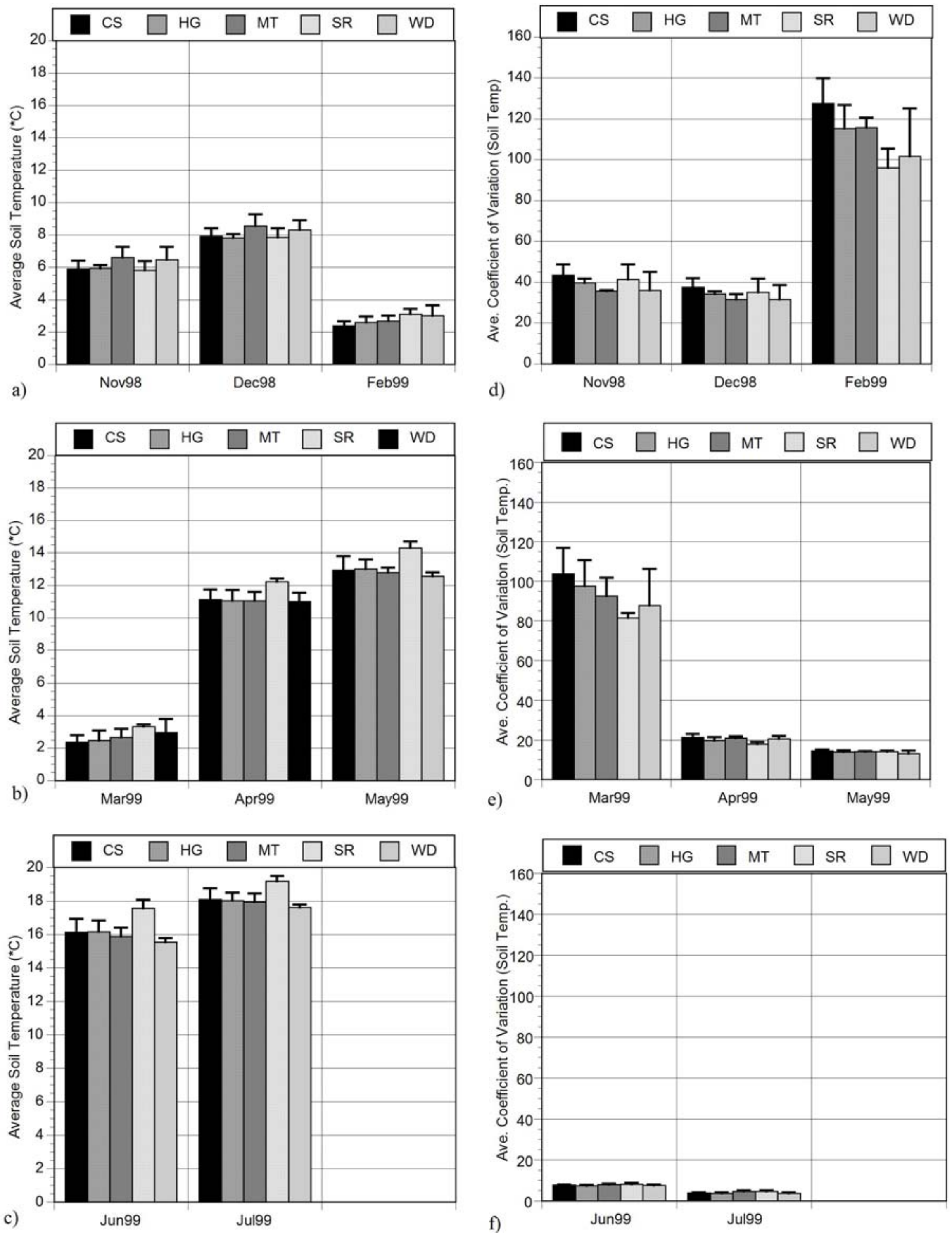

Figure 3.5. a-c) Average monthly soil temperature and d-f) average coefficients of variation in monthly soil temperature in microhabitats (n=3 data loggers/microhabitat) in 1999 in two-age regeneration stands at Wine Spring Creek watershed, N.C.

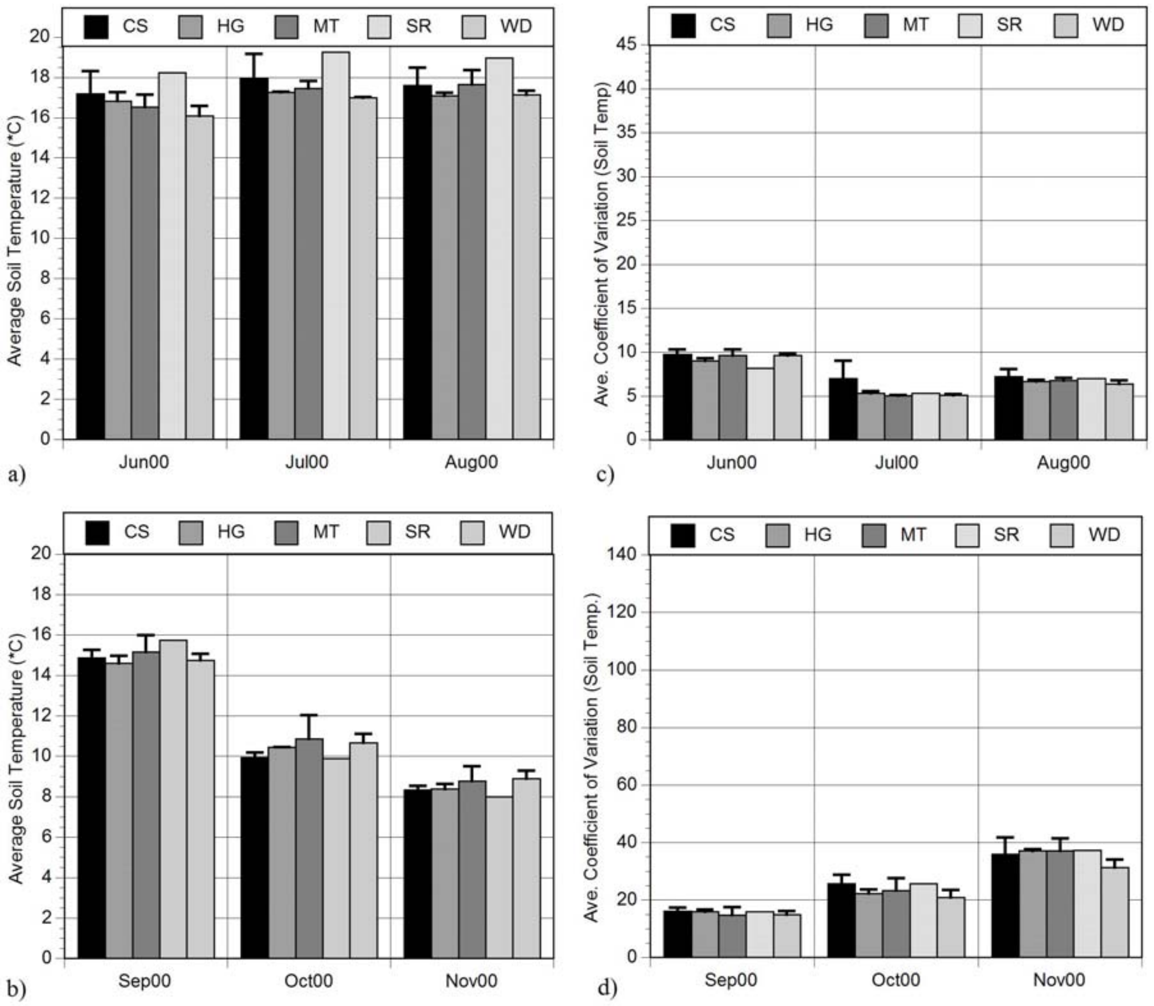

Figure 3.6. a-b) Average monthly soil temperature and c-d) average coefficients of variation in monthly soil temperature in microhabitats (n=3 data loggers/microhabitat) in 2000 in two-age regeneration stands at Wine Spring Creek watershed, N.C.

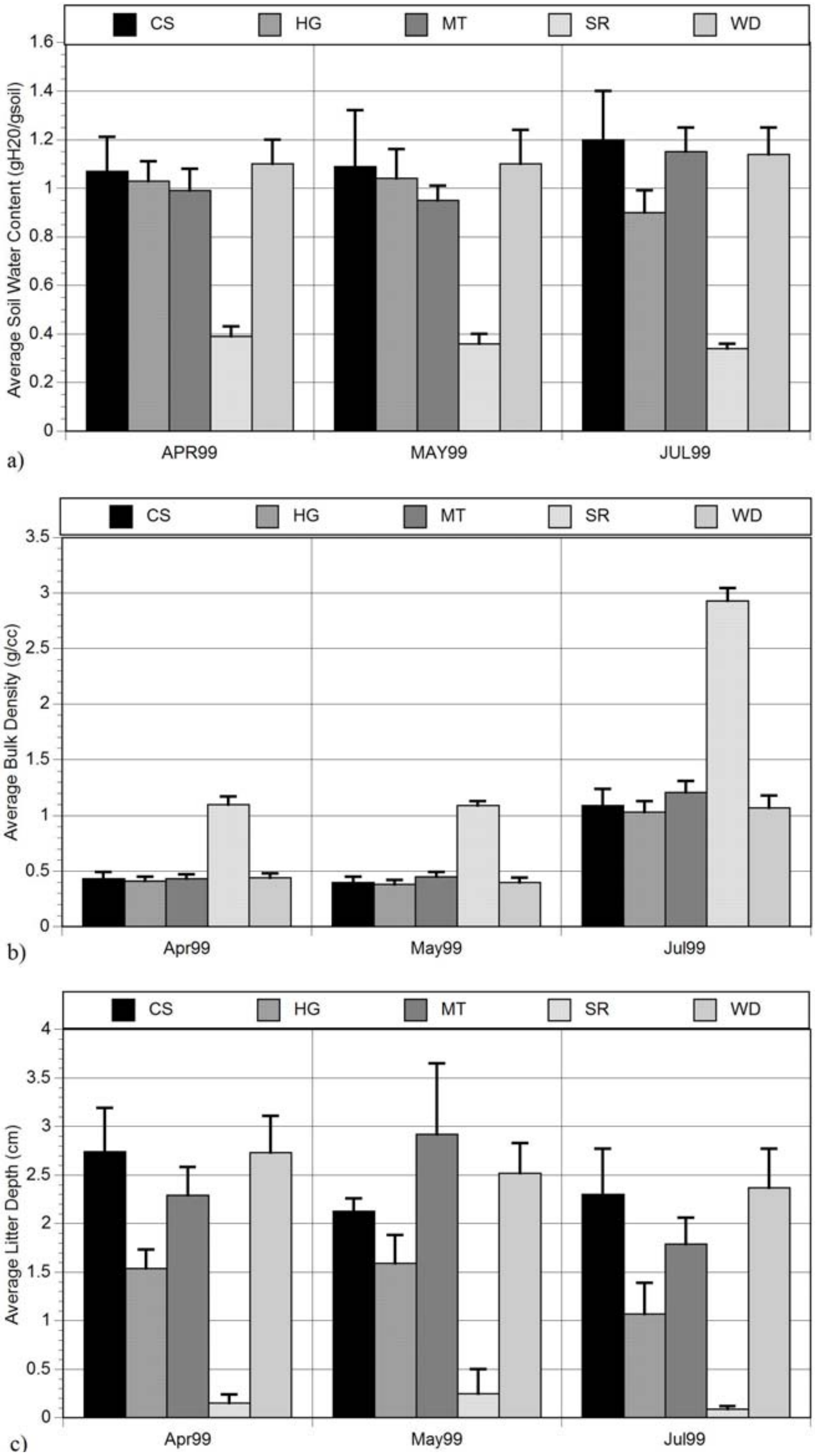

Figure 3.7. Average a) soil water content, b) bulk density, and c) litter depth within microhabitats (n=3/microhabitat) in two-age stands during spring 1999 at Wine Spring Creek watershed, N.C.

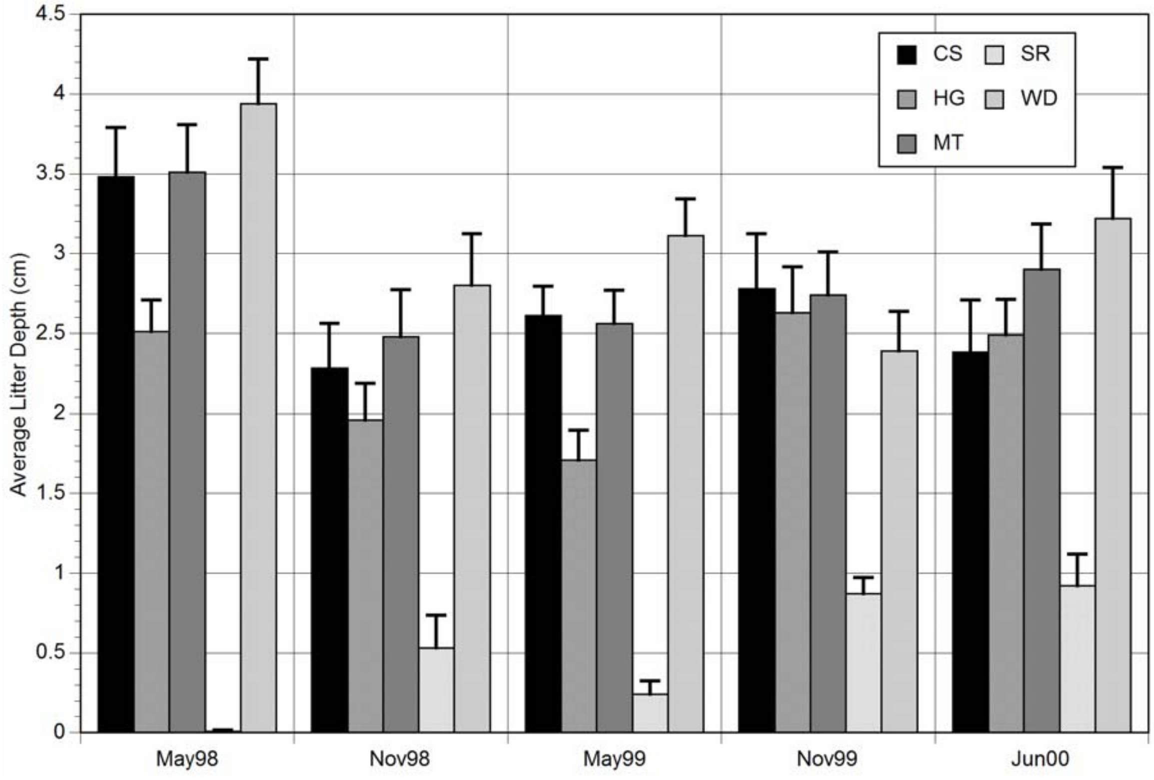

Figure 3.8. Average litter depth (cm) within microhabitats (n=50/microhabitat) in the two-age regeneration stands during the spring and fall microarthropod sample dates at Wine Spring Creek watershed, N.C.

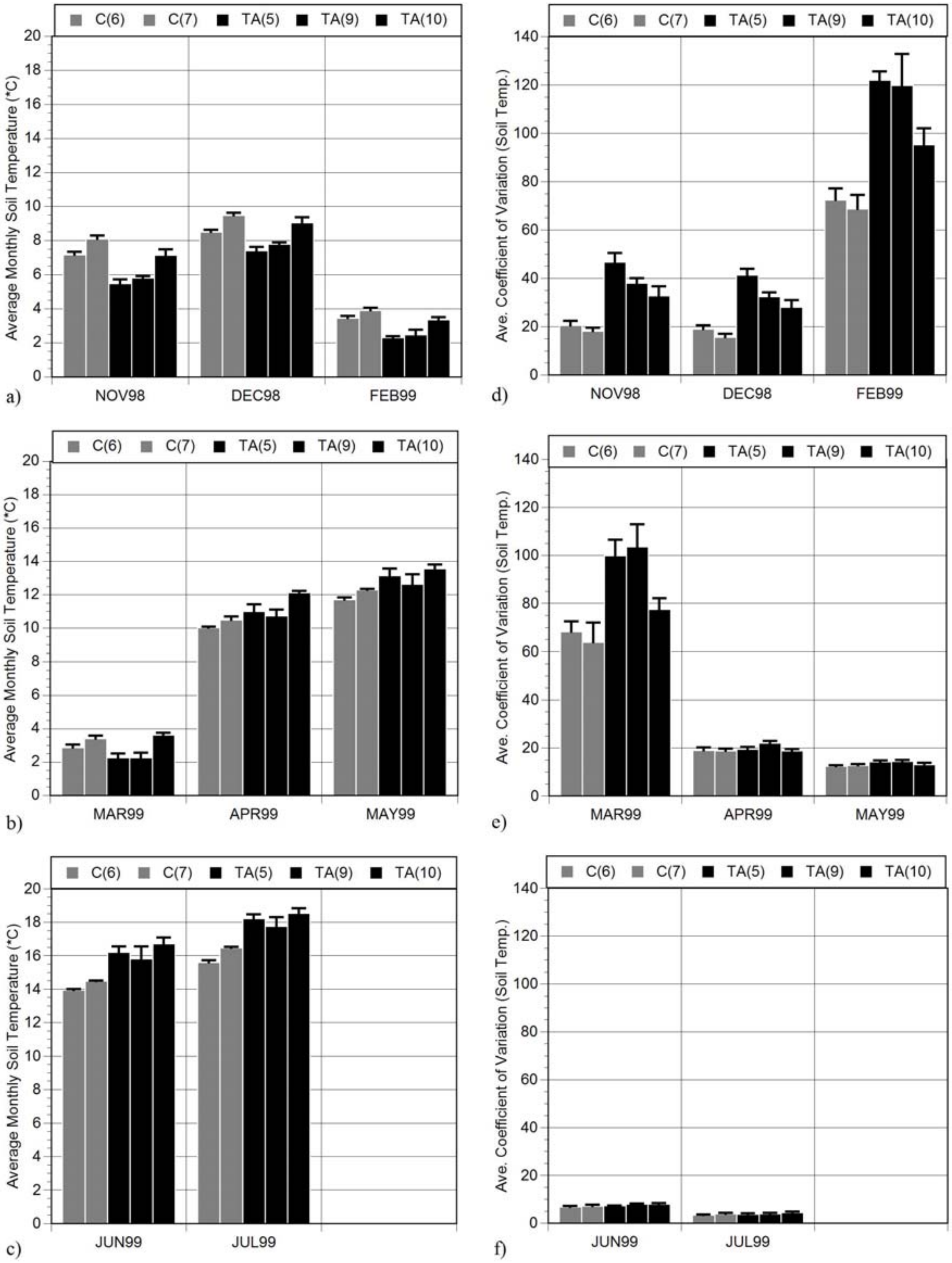

Figure 3.9. a-c) Average monthly soil temperature and d-f) average coefficients of variation in daily soil temperature (n=5/stand) in 1999 in two-age regeneration and control stands at Wine Spring Creek watershed, N.C.

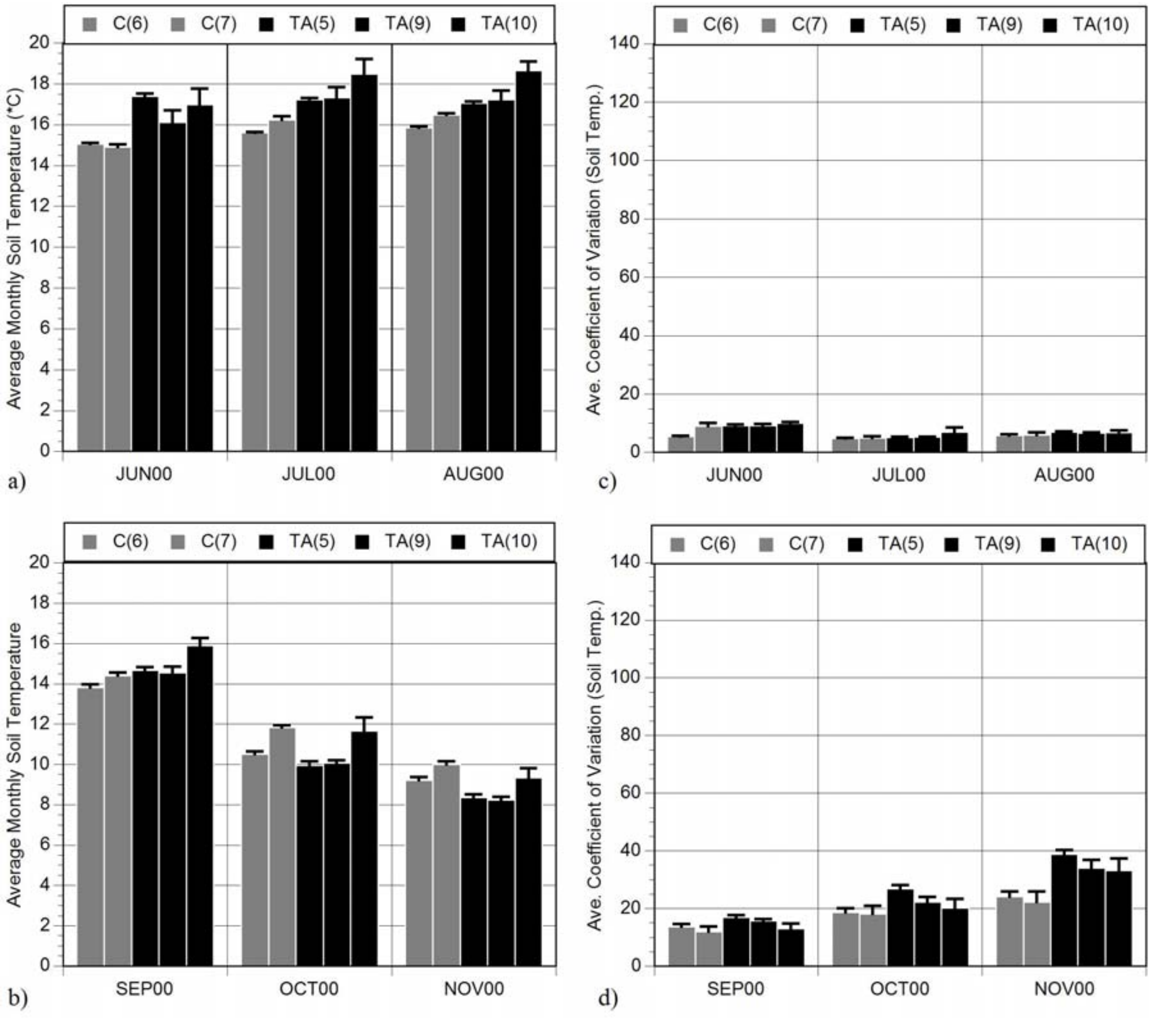

Figure 3.10. a-b) Average monthly soil temperature and c-d) average coefficients of variation in monthly soil temperature (n=5/stand) in 2000 in two-age regeneration and control stands at Wine Spring Creek watershed, N.C.

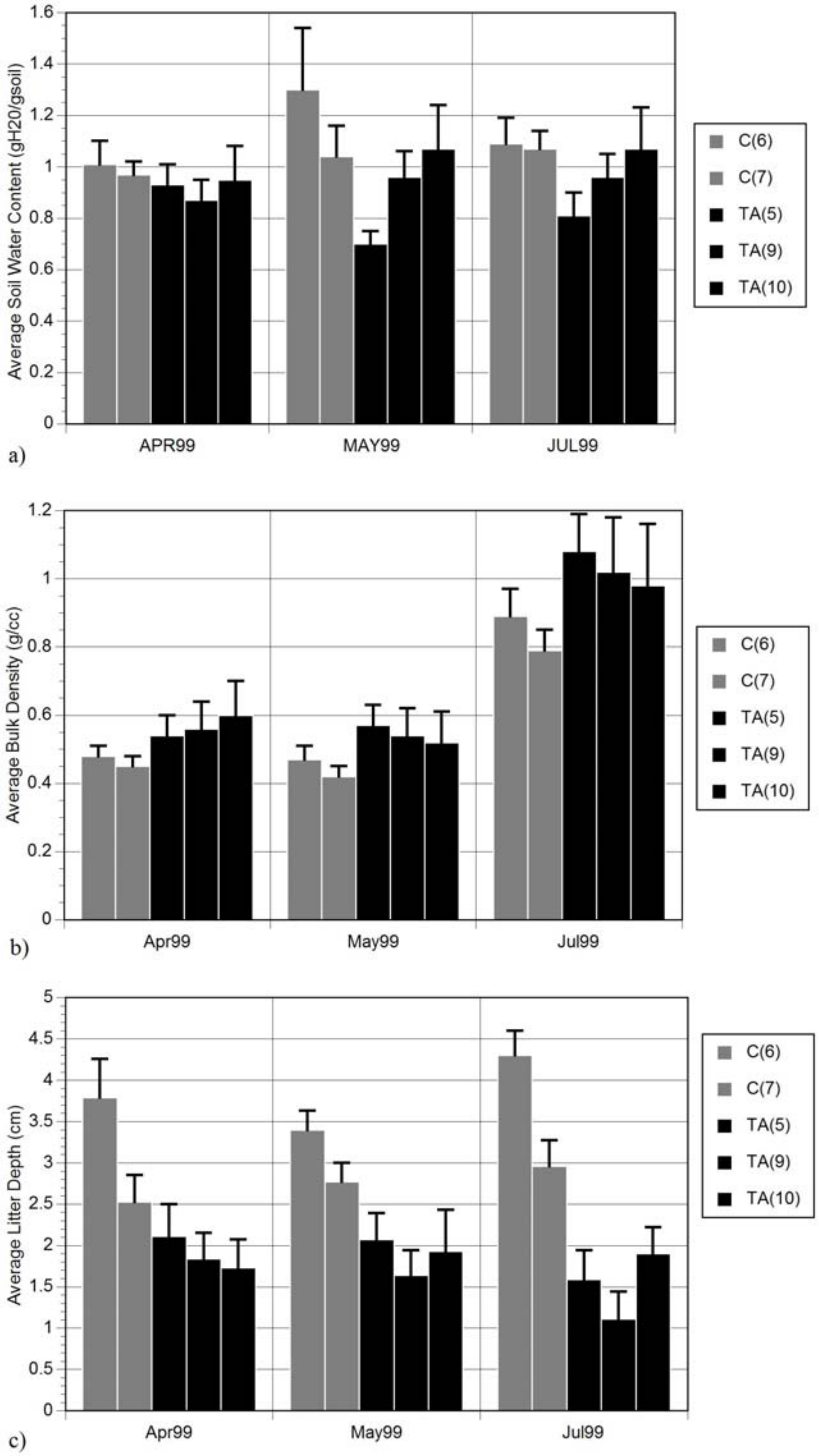

Figure. 3.11. Average a) soil water content, b) bulk density, and c) litter depth between control stands and among two-age regeneration stands (n=15/stand) at Wine Spring Creek watershed, N.C.

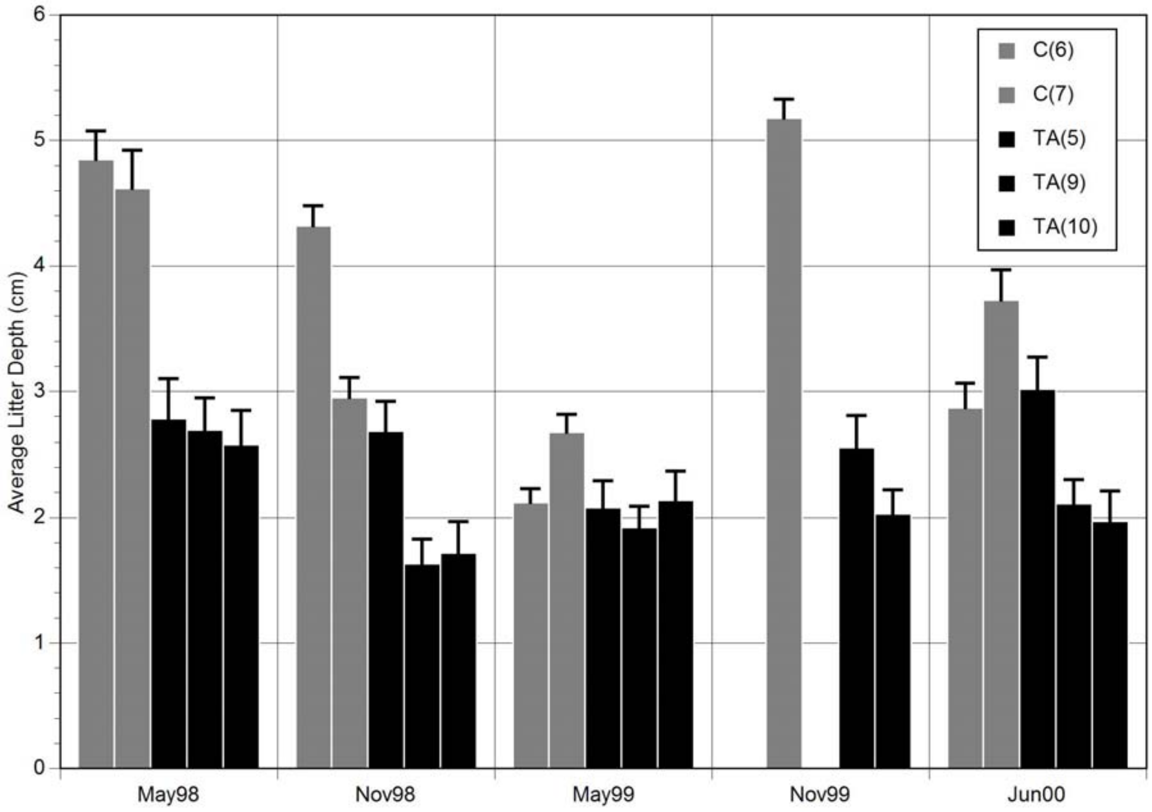

Figure 3.12. Average litter depth (cm) between controls and among two-age regeneration stands during the spring and fall microarthropod sample dates (n=250/date) at Wine Spring Creek watershed, N.C.

CHAPTER 4

RESPONSE OF SOIL MICROARTHROPODS (COLLEMBOLA, ACARI) TO TWO-AGE REGENERATION IN THE SOUTHERN APPALACHIANS[1]

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[1] Madson, S.L. and D.C. Coleman. To be submitted to *Applied Soil Ecology*.

Abstract

Forest stands are harvested on a scale of several hectares, whereas most microarthropods will spend their entire lives within a scale of several meters. Rarely is this mismatch between spatial scales accounted for when examining the response of soil microarthropods to forest harvesting methods, such as two-age regeneration treatments. Microhabitats, for example mature trees left as refugia, coarse woody debris piles, grassy clearings, shrubs, and coppices, are created or exacerbated by the harvesting process. In other ecosystems, such as Mediterranean scrub lands or Pacific Northwest forests, microhabitats have been shown to be a determining factor in microarthropod community composition. We examined microhabitats as a common spatial unit to assess the response of soil microarthropods to two-age regeneration treatments within hardwood stands at Wine Spring Creek Watershed in the southern Appalachians. Microarthropods were extracted using modified Tullgren extractors and sorted to sub-order. Natural spatial heterogeneity in the soil microarthropod communities was high in both the control and cut sites. Soil microarthropod abundance decreased in the two-age regeneration treatments, with the exception of the immature oribatids, which increased, and the oribatids, which remained the same. Most of the microarthropod taxa showed the greatest response to harvesting when examined at the scale of microhabitats. Microarthropod abundance was lowest in skid roads and was highest in coppiced and mature tree microhabitats. Using microhabitats as a common spatial scale between microarthropod communities and harvested forest stands appears to be a useful tool in elucidating treatment effects within the high natural heterogeneity of microarthropod communities in forest stands.

Keywords: soil microarthropods, oribatids, collembola, insects, spiders, mites, myriapoda, pseudoscorpions, protura, two-age regeneration, hardwood forests, harvesting, southern Appalachians, spatial scale

Introduction

Timber production and recreation historically have been two of the dominant management goals for forested public lands. During the last decade, management goals have shifted to encompass the need to maintain ecosystem processes, species diversity, and habitat structure of forested lands, while continuing timber production (Franklin 1993, McComb *et al*. 1993, Hopwood 1991, Caza 1993). The need for public agencies to seek management strategies to maintain or increase species diversity while allowing timber production to continue on public lands and public outcry has led to a shift from traditional silvicultural practices, like clear-cutting, to selection harvesting techniques, collectively known as regeneration treatments, as the dominant forest management practice.

Regeneration treatments are the silvicultural practice of reducing stand density through the partial removal of the overstory canopy (Tappeiner 1992). This practice has been recognized as the primary tool for land managers to meet the specific objective of producing habitat and maintaining species diversity, while continuing timber production (Tappeiner 1992, FEMAT 1993, Record of Decision 1994, Cole 1996). Regeneration treatments release the remaining trees from crowded stands, allowing the trees to grow larger and healthier. Site regeneration is enhanced and occupancy by plant species hitherto restricted to other habitats is facilitated.

Two age cuts are regeneration treatments that generally harvest 60-70% of the standing basal area within a stand. The remaining trees provide shade, seed, and mycorrhizae and as well as serving as refugia for animals. Under the partial shelter of the remaining trees, the next cohort of advance regeneration is established. Few studies have compared the effect of two-age cuts on biodiversity to other silvicultural practices.

Arthropods are integral to a functioning forest ecosystem and perform key roles as detritivores, herbivores, predators and prey. Microarthropods, in particular the oribatid mites (Acari: Oribatida), are the most abundant and diverse animals living in soil and litter environments. Soil and litter arthropods aid in the regulation of rates of nutrient cycling, decomposition and energy flow (Petersen and Luxton 1982, Wallwork 1983, Seastedt 1984, Persson 1989, Wardle and Giller 1996). Disturbance of microarthropod communities has the potential to alter or disrupt these processes.

Silvicultural practices like clear-cutting have been shown to reduce soil microarthropod populations in the litter and upper soil horizons over 50% (Seastedt and Crossley 1981). Reduction in numbers of the microarthropod community can still be discernible 8 years after cutting (Blair and Crossley 1988). Compaction of the soil, due to harvesting or trampling, also reduces populations of soil microarthropods (Usher 1985, Vtorov 1993).

The effects of 'intermediate' disturbances, such as regeneration treatments, can be difficult to discern due to the resilience of organisms or stands, the history of a site, or geologic, geographic and/or environmental heterogeneity that overwhelm management effects (Usher 1985, Bailey *et al*. 1998, Madson 1997). To detect the effect of regeneration treatments upon soil microarthropod community composition, it is therefore necessary to establish robust measures of the ‘natural’ heterogeneity and variability within forested ecosystems.

Diverse oribatid community assemblages, also characterized by high abundance, have been positively correlated with high soil moisture, intermediate soil temperatures, and high organic matter (Fujikawa 1970, Wallwork 1970, Usher 1976, Santos *et al*. 1978, Vannier 1987, Anderson 1988, Whitford 1989, Asikidis and Stamou 1991, Cancela da Fonseca *et al*. 1995, Scheu and Schulz 1996). Soil bulk density has been negatively correlated with numbers of soil microarthropods (Wallwork 1970, Usher 1985). Torgersen *et al.* (1995) also found a negative correlation between numbers of microarthropods and increasing distance from individual trees. Distinct microarthropod assemblages have been found in microhabitats within a single site when the microhabitats were characterized by differing values of moisture, temperature, soil organic matter, and the presence or absence of coarse woody debris or live trees (Aoki 1967, Asikidis and Stamou 1991).

Disturbance enhances or maintains the occurrence of strongly delineated microhabitats within forested systems. Microhabitats, with varying degrees of temperature, moisture and soil organic matter accumulations, in turn alter the community composition of oribatid mite assemblages. Few studies have successfully quantified the effects of regeneration treatments, in particular two age cuts, upon the formation of distinct microhabitats and oribatid assemblages. The goal of this study is to characterize changes in the abundance and distribution of litter-dwelling oribatid mites in response to the silvicultural practice of two age regeneration.

The objectives of this study are multifold. The first objective is to establish the natural variation and spatial heterogeneity within microarthropod communities at Wine Spring Creek watershed. The second objective is to compare the abundance of microarthropod communities within control sites to regeneration stands. The third objective is to establish the correlation between microarthropod communities and microhabitat types. It is hypothesized that soil and litter under mature trees and coarse woody debris will support the highest abundance of microarthropods, that coppices, shrubs and herbaceous clearings will have a relatively lower abundance of microarthropods compared to the previous microhabitat types, that the herbaceous clearings and woody debris piles will yield distinct community assemblages from the other microhabitats, and, lastly, that skid roads will have the lowest abundance of microarthropods.

Materials and Methods

Site Description

The study was conducted at Wine Spring Creek Watershed (latitude: $83^{o}35'43''$ W, longitude: $35^{o}10'36''$ N) in the Nantahala National Forest, Wayah Ranger District, North Carolina, approximately one hour’s drive (60 km) northwest of the Coweeta Hydrologic Laboratory in Otto, NC. The 1820 ha basin is a demonstration project of ecosystem management, initiated in the early 1990’s, that provides an integrated, interdisciplinary ecosystem approach to planning, research, and management. Eleven sites were selected by ground surveys conducted by USFS employees in northern red oak-flame azalea (Quercus rubra-Rhododendron calendulaceum) dominated communities on northwest facing slopes.

McNab and Browning (1993) classified these ridges as dry, high-elevation, with moderate to steep slopes. Mean monthly temperature ranges from 3°C in January to 22°C in July. Precipitation averages 60 inches annually and is evenly distributed throughout the growing season, with only a little falling as snow. Growing season is 180 days. The average temperature is lower, growing season shorter, and wind speeds higher at these sites relative to lower elevations in the watershed. Soil parent material consists of a metamorphic formation of biotite gneiss, biotite, garnet gneiss, and amphibolite. Soils are mapped as Wayah series and the A horizon is classified as black sandy-loam, with 18% organic matter (Soil Survey Division 2001).

The study sites ranged in elevation from 1,380-1,580 m and were 4.0-6.6 ha in size. The Forest Service acquired the watershed in 1912 after it had been logged over. The stands selected for this study were mature, between 70-80 years old, with minimal disturbance since acquisition by the Forest Service (W. J. Culpepper, personal communication). For a full site description, see Elliott and Hewitt (1997) and McNab and Browning (1993).

A silviculturist with the Wayah District office assigned each site to one of three regeneration treatments (two-age cut, shelterwood, group selection), with three replicates each, or to the control (uncut), with two replicates. Criteria used to assign treatment type included species composition, geographic location, and proximity to roads (W. J. Culpepper, personal communication). This study was performed in the two-age cuts (sites 5, 9, 10) and control sites (sites 6, 7). The regeneration treatments were harvested in the summer of 1997. The stands were contract sold to a local timber company and harvested using a skidder unit. The skid roads were bladed with a bull-dozer and reseeded after harvesting was completed. In November of 1997, the stands were site prepared for natural regeneration by chainsaw felling of undesirable or damaged residual stems. After harvesting and site preparation, 90% of vegetation in the stands had been removed. The two-age regeneration cuts had a 3.67 m^2 residual basal area per hectare (W. J. Culpepper, personal communication).

Microhabitats

The harvested stands were characterized by distinct microhabitats created by the regeneration treatment. The first microhabitat consisted of remaining mature trees (MT) scattered throughout the stand, representing approximately 30% of the original stand basal area. The second microhabitat consisted of coppices from the harvested trees and shrubs, which were predominantly flame azalea (CS). Due to a low chip mill market at the time of harvest, boles were stripped of the crown and branches on site and the slash left behind. Large piles of coarse woody debris (WD), reaching sizes of two meters in height and three meters in diameter, were found throughout the stand. Clearings within the stand were characterized by herbaceous growth (HG), including grass, ferns, and other perennial herbaceous plants. Lastly, the skid roads (SR) used for harvesting the stand covered approximately 5% of the stand.

Microarthropods

The population of interest was litter-dwelling microarthropod assemblages within microhabitats (CS, HG, MT, WD, SR) of two-age regeneration cuts and in the control stands. In all the stands, a 25-m buffer zone was delineated to reduce edge effects. A 25 x 165 m grid (4125 m^2) was established using a random starting point within each of the two-age stands. The grid was laid out using the same orientation in each harvested site for the width (214^o) and length (298^o) of the grid. Fifty points within each grid were randomly selected and assigned to microhabitat classes (ten points per microhabitat). If a point did not fall within the selected microhabitat, the nearest representative microhabitat was sampled. Since the control stands did not exhibit distinctly delineated microhabitats, a regularly spaced grid of 50 sample points was established on a triangular lattice. Sample points were five m apart.

To measure the microarthropod communities, a single soil core of 4.5-cm diameter and 5.0-cm depth was taken at each point. Each core included the litter layer and O horizon. The cores were returned to the lab and heat extracted using a modified Tullgren extractor (Blair and Crossley 1991) for one week. The samples were stored in 70% alcohol until processed. Samples were examined under a dissecting microscope and sorted to suborders. The microarthropod communities were sampled in the spring (late May, early June) of 1998, 1999, and 2000 (n=10/microhabitat, n=50/stand, n=250/season, n=750/study). A total of 731 samples were processed. Nineteen cores were lost due to sampling or processing errors.

Statistical analysis

The data collected were count data of microarthropod abundance at each point. Exploratory data analysis using histograms generated in S-PLUS (2001) showed the data were non-parametrically distributed, with a long-tail to the right (Fig. 4.1). For analyses requiring normality, a log10(x+1) transformation was used, to avoid the problem of observations with zeroes.

The natural spatial heterogeneity within the stands and the degree of spatial correlation along a distance gradient was evaluated using two methods, the empirical variogram and the Mantel test, on count data from the controls. Empirical variograms were performed individually for each taxon by year and data were log10 transformed before analysis. The empirical variogram dialog was run with the robust method selected because of the high number of outliers remaining even after transformation in S-PLUS (2001) to describe how the data were related with distance. Next, the model variogram dialog was used to determine the best fit of the model and parameter values.

The Mantel test was run using the ordination software package PC-ORD (McCune and Mefford 1999) to test the null hypothesis of no relationship between abundance data and sample location. The Mantel test compared untransformed count data from the control stands (n=50) for each year against the grid location (x, y) for each point. Unlike the variogram analysis, the Mantel test examined the taxa at each point together. An asymptotic approximation was used to evaluate the test statistic.

Generalized linear models (SAS 1999, PROC genmod) were run to test for differences in count data among treatments, years, stands, and microhabitats and to determine interaction effects of the independent variables upon the count data. The generalized linear model was chosen because it required no assumptions about distributions, which allowed untransformed, non-parametric data to be used as the response variable. The Poisson regression model with a log link function was selected because the response variable was count data (Insightful 2001).

Results

Natural spatial heterogeneity

Spherical variogram models yielded the best fit visually, and consistently had the lowest residual sum of squares, of the theoretical variogram models analyzed for all stands and years. Model results on the relationship between oribatid abundance and distance between sample points varied widely from year to year, site to site. The spherical variogram for site 7 in the spring of 1998 was a flat line, indicating no spatial dependence between oribatid abundance and location of the sample point (Fig. 4.2). Site 6 in 1998 and site 7 in 2000 both showed a positive trend with increasing distance. The remaining three variograms, site 6 in 2000 and both sites in 1998, had a range between 9-12 m, indicating spatial dependence between oribatid abundance and distance between samples as less than 12 m. The Mantel test statistic was not significant for any of the sites or years, indicating no relationship between community abundance and spatial proximity (Table 1). Overall, the data indicate a very weak relationship between distance and oribatid density.

Treatment differences

Collembola, prostigmata, mesostigmata, insect, proturans, myriapoda, and spider abundance (Fig. 4.3a-g.) were significantly higher in the control sites ($p<0.0011$). Immature oribatid abundance was significantly higher in the two-age cut sites ($p=0.0001$) (Fig 4.3h.). Oribatid ($p=0.61$) and pseudoscorpion ($p=0.46$) abundance (Fig. 4a-b.) were not significantly different between treatments. Differences between treatments were consistent from year to year for all taxa, except the pseudoscorpions.

Microhabitat differences

Within the two-age cuts, there were significant differences among microhabitats for all taxa ($p=0.0001$), except the myriapoda, proturans, and pseudoscorpions, which occurred too rarely within the stands to make a comparison among microhabitats. Differences among microhabitats were consistent from year to year for all taxa, except for the collembola and insects (Fig 4.5a-f.). The mature tree microhabitat had the greatest average abundance of taxa. All taxa were most abundant at the base of mature trees (Fig. 4.6a-d.), except the prostigmata, the proturans, myriapoda, and spiders. The prostigmata were most abundant in the herbaceous microhabitat (Fig. 4.6e.), but this was due to the abundance of one subgroup of prostigmata, which comprised nearly half of all prostigmata counted. When this group was eliminated from the analysis, the prostigmata were most abundant near mature trees (Fig. 4.6f.). The proturans, myriapoda, and spiders were most abundant in the woody debris piles (Fig. 4.7a-c). All taxa were least abundant in the skid roads, with the exception of the spiders, which were less abundant in the herbaceous areas.

Year differences

Abundance of all taxa, except the pseudoscorpions, was lowest in 1998, the year following harvesting. There were significant differences in the abundance of all taxa among years ($p<0.0031$); except for spiders ($p=0.15$) and pseudoscorpions ($p=0.75$) (Fig 4.8a-b). Abundance of collembola, oribatids, mesostigmata, myriapoda, insects, and prostigmata was significantly higher in 1999 (Fig 4.9a-e, 4.10a). Removal of the dominant subgroup of prostigmata shifted this result so that the remaining prostigmata groups were more abundant in 2000 (Fig. 4.10b). Immature oribatids and proturans were significantly greater in abundance in 2000 (Fig. 4.11a-b).

Stand differences

There were significant differences among stands in the densities of collembola (p=0.0001) (Fig. 4.12a-c), oribatids (p=0.0001) (Fig. 4.12d-f), mesostigmata (p=0.0001) (Fig. 4.13a-c), prostigmata (p=0.0001) (Fig. 4.13d-f), insects (p=0.0001) (Fig. 4.14a-c), and pseudoscorpions (p=0.0014) (Fig. 4.14d-f), but differences were not consistent from year to year. Immature oribatids (p=0.0001), proturans (p=0.0007), myriapoda (p=0.0001), and spiders (p=0.0001) showed significant differences that were consistent from year to year. Immature oribatids were consistently more abundant in sites 9 and 10 and lowest in site 5 (Fig. 4.15a). Proturans were most abundant in site 5 and then the control sites (Fig. 4.15b). The myriapoda and spiders were most abundant in the controls (Fig. 4.15c-d). The dominant prostigmata subgroup was significantly more abundant in the control stands, but site 7 had nearly double the number found in site 6.

Discussion

Natural spatial heterogeneity

The weak spatial correlation of microarthropod communities at distances between 9-12 meters and the variation of this result in time and space suggest that there is a high natural heterogeneity of communities located five meters or further apart in hardwood stands in the southern Appalachians. Community abundance and composition is extremely varied over short distances within these stands, which has the potential to obfuscate treatment effects, which generally occur over a scale of hectares. These results are consistent with previous studies (Aoki 1967, Fujikawa 1975, Usher 1976, Schenker 1984, Norton 1990) that suggest that microarthropods aggregate in clumped distributions horizontally within the soil. Hansen (2000) concluded that assemblages are determined by local habitat attributes and that community dynamics can be autonomous within a meter square. While local soil temperature, moisture, litter quality and quantity may determine community dynamics over short distances (<1m), the spatial correlation seen to occur at 10-12 meters in this study may be the contribution of larger habitat structures, influencing areas greater than one m^2, such as coarse woody debris and vegetation patches, to community dynamics. The variation of this result in time and space suggests that local processes, such as litter availability, quality, and decomposition rate, remain the stronger determinants of microarthropod community dynamics.

Treatment effects

The significant decrease in the abundance of most of the soil taxa, including the collembola, prostigmata, mesostigmata, hexapoda, protura, myriapoda, and spiders, in the harvested stands in the first three years post-harvest is consistent with most previous studies examining the response of soil microarthropods to harvesting methods (Abbott *et al*. 1980, Bird and Chatarpaul 1986, Blair and Crossley 1988, Hoekstra *et al*. 1995, Huhta *et al*. 1967, Huhta 1976, Madson 1997, Marra and Edmonds 1998, Seastedt and Crossley 1981, Vlug and Borden 1973). Decreases in abundance of taxa have been attributed to many factors including decreased food resources (Huhta 1976), erosion (Marra and Edmonds 1988), high temperatures (Abbott *et al*. 1980), vertical distribution and amount of organic matter (Seastedt and Crossley 1981), low moisture, compaction (Bird and Chatarpaul 1986), and high pH (Vlug and Borden 1973).

The similarity in the abundance of oribatids between treatments and the increase in immature oribatid abundance in the two-age regeneration stands has not been reported previously. Huhta *et al*. (1967) and Huhta (1976) reported an initial increase in oribatid density in the first year after harvest, but this was followed by a marked decrease in abundance such that the uncut sites had a greater abundance than the harvested sites. The increase in immature oribatids may reflect the availability of additional food resources and habitat niches to adult oribatids that are usually occupied by other functionally-similar soil taxa, such as the collembola. It may also reflect a release from predation as the soil arthropod predator functional groups, such as the mesostigmata, centipedes, and spiders, all showed decreases in abundance. It is difficult to explain why oribatid abundance did not decrease, unlike the other taxa or the findings of other studies. One possible explanation is the high diversity of species of oribatids found in the southern Appalachians. It is possible that species dominance within the oribatid community shifted as has been seen in other studies (Bird and Chatarpaul 1986, Huhta *et al*. 1967, Seastedt and Crossley 1981), but abundance remained the same as species better adapted to the new conditions within the stand reproduced. A second possibility is that at the time of harvest (mid to late summer), the oribatids had migrated vertically within the soil, as seen in other studies (Wallwork 1970, Norton 1990), thus finding refugia from the harvesting. Soil temperatures during the summer months can be extremely high, reaching 24^{o}C in July and August in the 0-5 cm layer (Madson 2003).

Microhabitat effects

The abundance of soil taxa did vary among microhabitats within the harvested stands. This is consistent with earlier studies that have indicated the importance of microhabitats in explaining the distribution of soil microarthropod assemblages (Aoki 1967, Asikidis and Stamou 1991). The most likely explanation for differences in microarthropod abundance among microhabitats is differences in microclimatic conditions. Degree of fluctuation in soil temperature, bulk density, and litter depth were significantly different among microhabitats (Madson 2003). Microarthropods were least abundant in the skid roads, which also had the greatest bulk density, the least litter, and the greatest variation in soil temperature. Microarthropods were most abundant near mature trees, which had a relatively deep litter layer, relatively moderate variation in soil temperature, and experienced the least amount of compaction due to forest harvesting. The areas immediately adjacent to mature trees were the least disturbed by forest harvesting. The belowground root system of the mature trees likely remained relatively intact and unaffected by harvesting, and may have created refugia for soil organisms, with relatively high food availability in the form of root exudates, bacteria, and fungal populations.

Year and stand effects

The low abundance of almost all taxa in 1998 is attributable to the harvesting process. The reason why soil arthropod abundance was higher across all sites in spring 1999 is unknown. Air temperature and rainfall were not significantly higher that season nor in the preceding years. Since this effect occurred across stands, it may be the reflection of a regular natural cycle of high and low abundance throughout time. The differences in soil arthropod abundance among stands of the same treatment can most likely be explained by natural variation, microclimate variation, geographic location, site geology, and stand history.

Conclusions

Two-age regeneration treatments do significantly decrease the abundance of most soil taxa, despite high natural heterogeneity. Microhabitats can serve as a common scale for understanding more specifically the response of soil microarthropods to forest harvesting. Differences in microclimatic conditions within microhabitats are most likely responsible for differences seen in species composition and abundance among microhabitats. Decreases in microarthropod abundance are related to disturbance intensity. The distribution and frequency of microhabitats within stands alters with harvesting method and intensity. Assessment of the pattern and frequency of microhabitats within disturbed stands may serve as a means of assessing the response of the soil arthropod communities to disturbance.

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Table 1. Mantel test statistics (r) and p-values for taxa abundance in control stands.

Site-Year	Mantel test statistic (r)	p-value
6-1998	- 0.045	0.51
6-1999	0.002	0.98
6-2000	- 0.096	0.21
7-1998	- 0.067	0.40
7-1999	0.071	0.35
7-2000	- 0.050	0.55

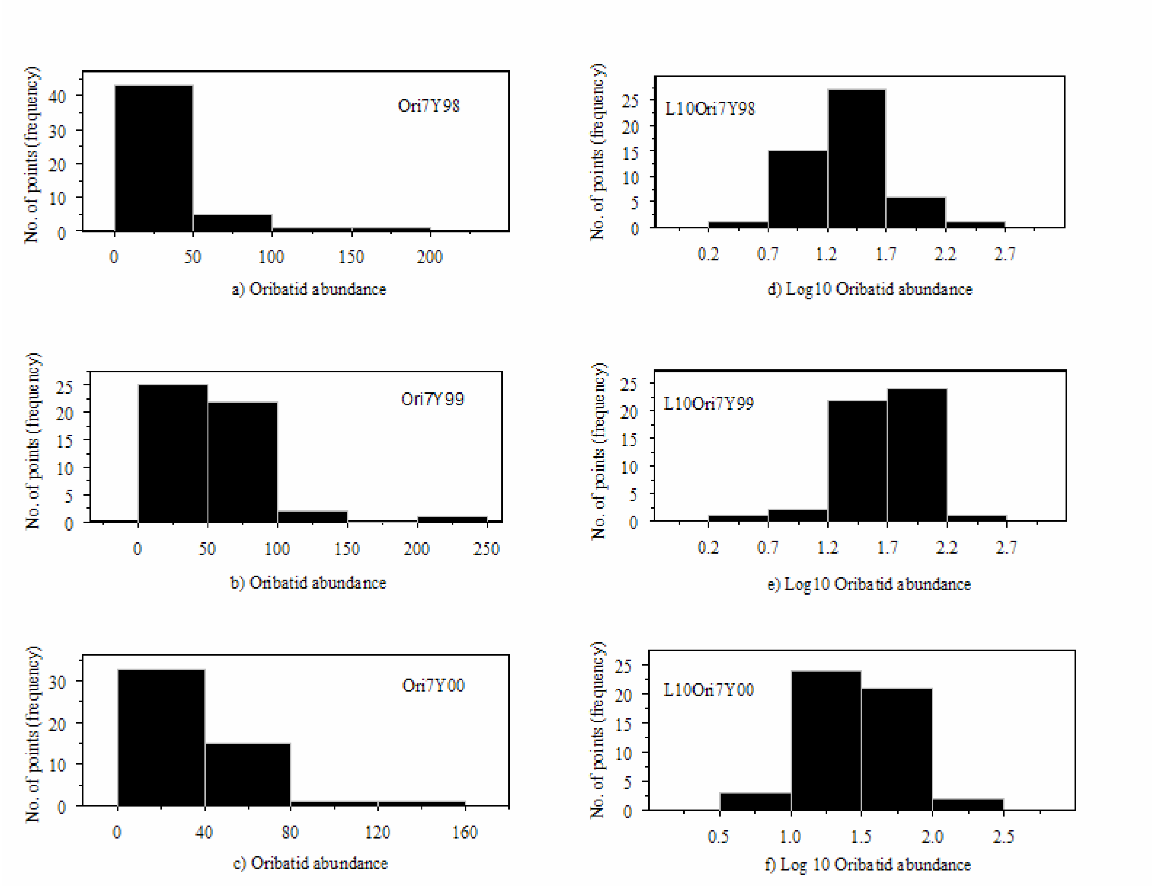


Figure 4.1. Histograms showing data distributions of oribatid abundance during the spring of 1998-2000 within control stand 7 before (a-c) and after (d-f) log10(x+1) transformation.

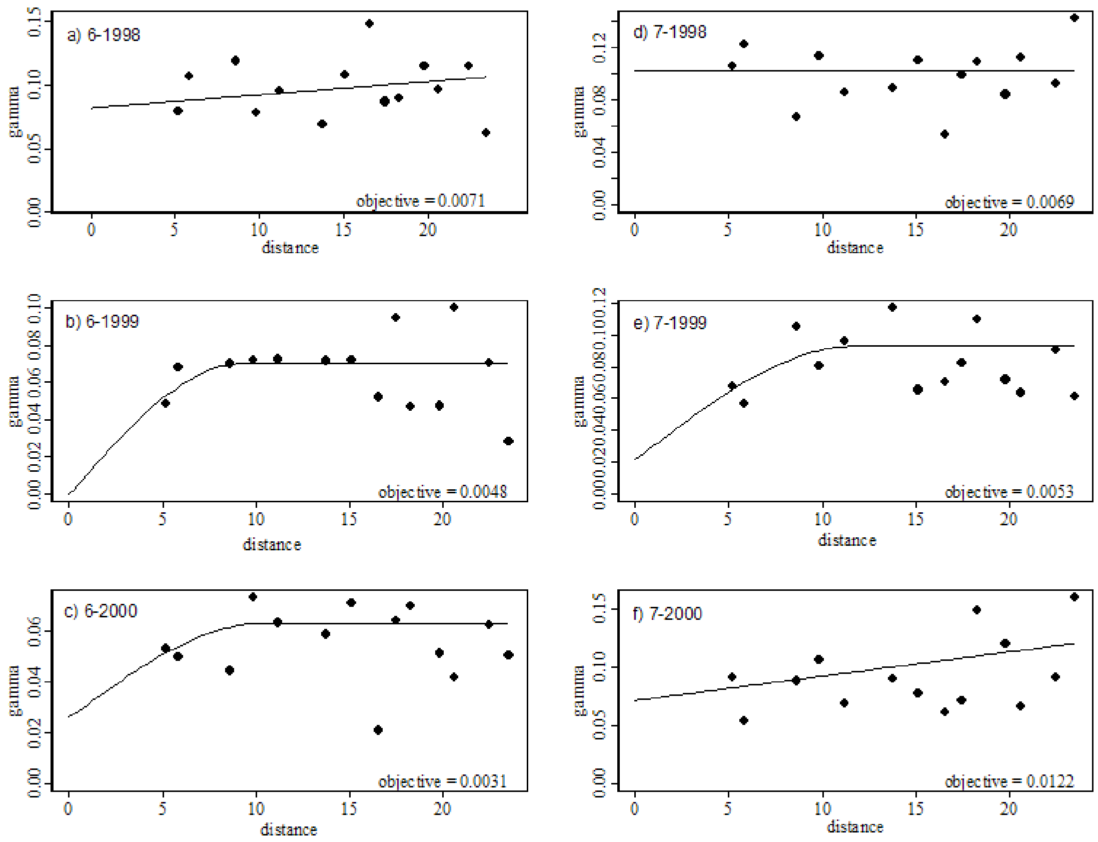
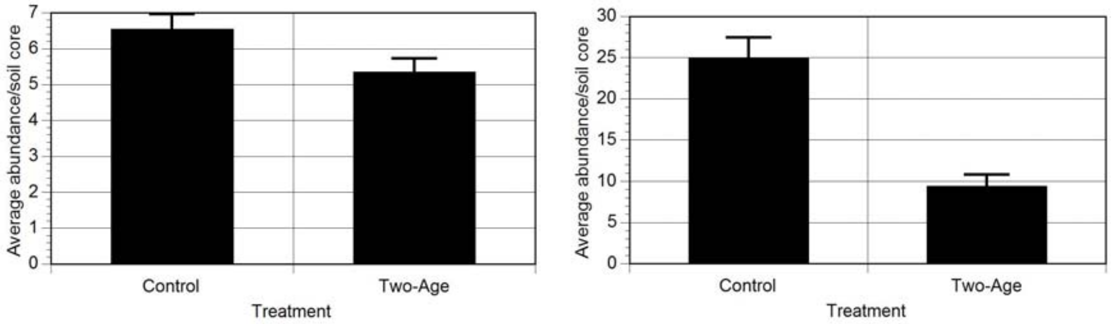
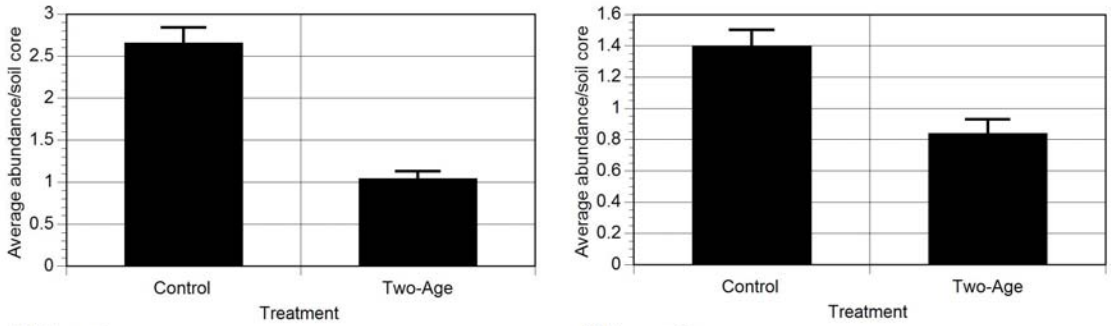


Figure 4.2. Spherical variogram models of oribatid abundance in the controls (site 6 a-c, site 7 d-f) correlated with spatial distance (m) for the spring of 1998-2000.



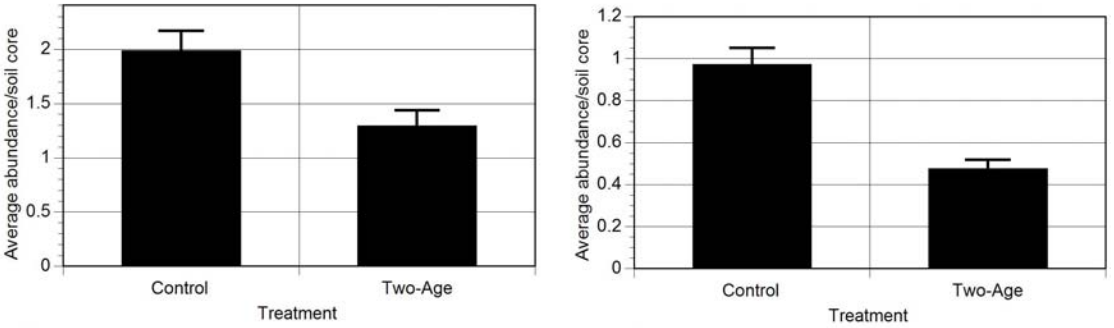
a) Collembola

b) Prostigmata



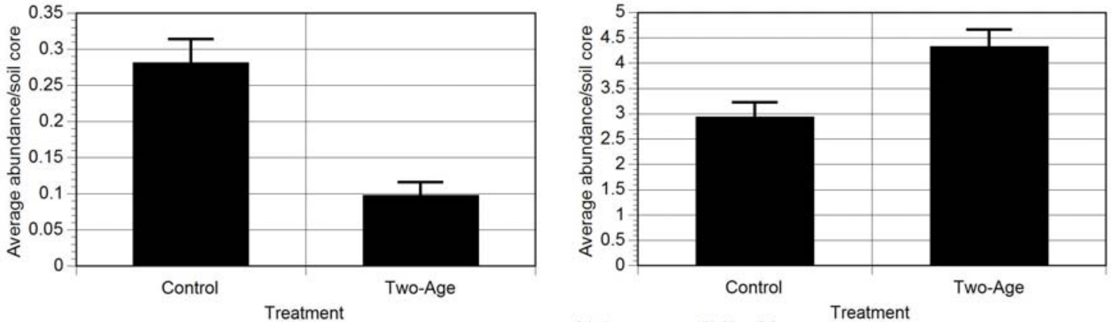
c) Mesostigmata

d) Hexapoda



e) Protura

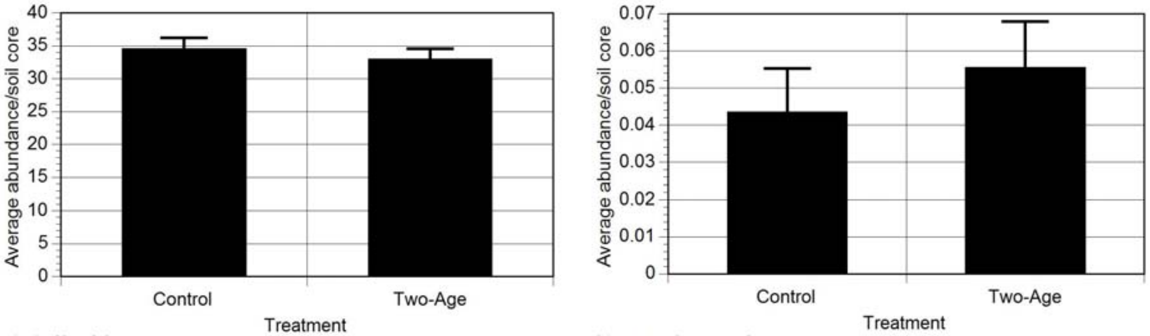
f) Myriapoda



g) Araneida

h) Immature Oribatida

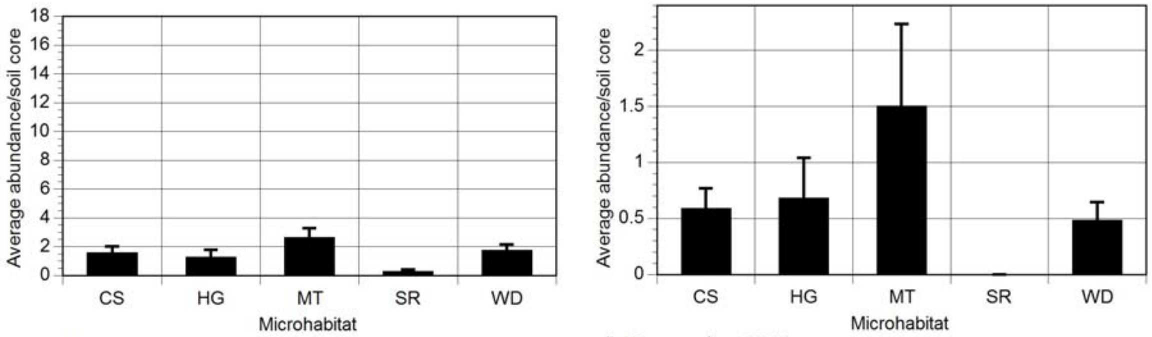
Figure 4.3. Differences in average abundance of soil microarthropods between two-age cut (n=450) and control sites (n=300), 1998-2000, at Wine Spring Creek watershed, N.C.



a) Oribatida

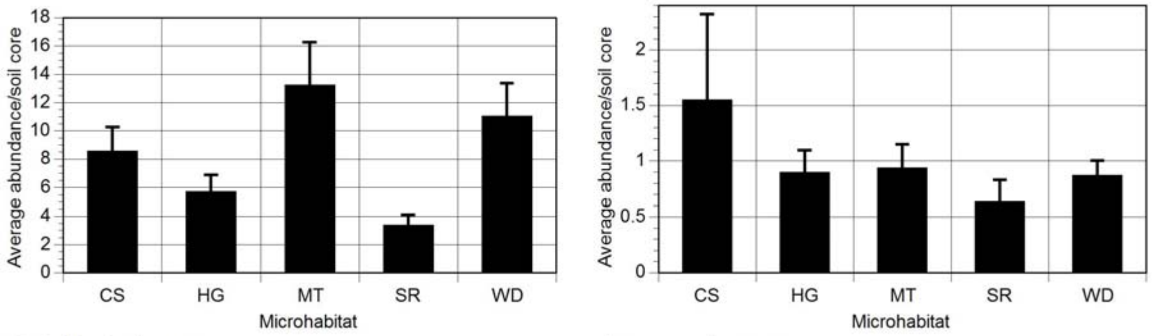
b) Pseudoscorpiones

Figure 4.4. Average abundance of oribatid mites and pseudoscorpions in two-age cut (n=450) and control (n=300) sites 1998-2000 at Wine Spring Creek watershed, N. C.



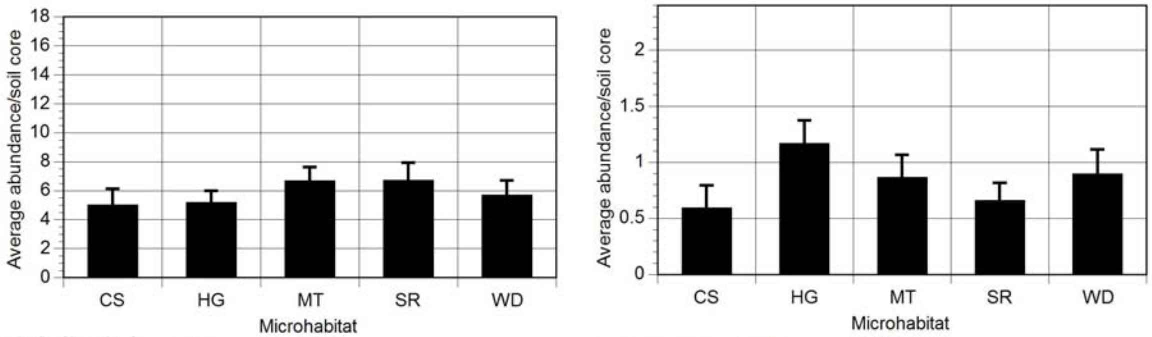
a) Collembola - 1998

d) Hexapoda - 1998



b) Collembola - 1999

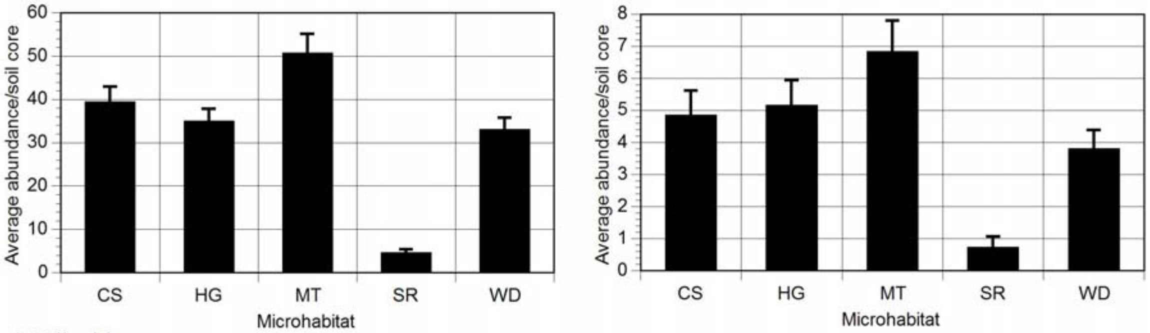
e) Hexapoda - 1999



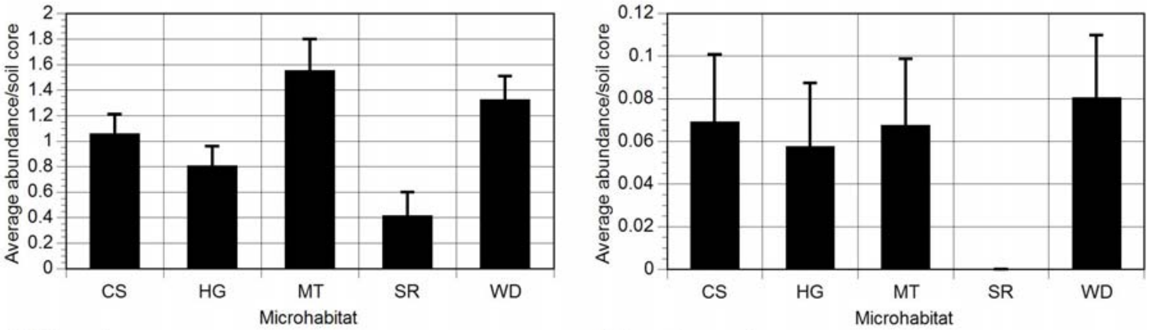
c) Collembola - 2000

f) Hexapoda - 2000

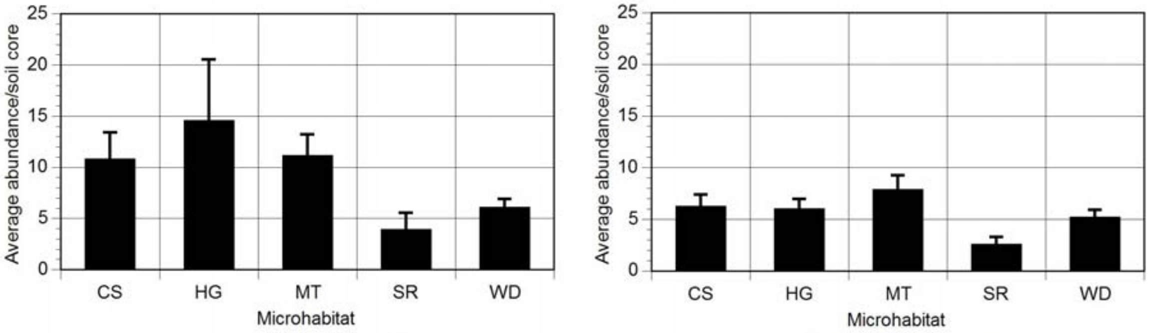
Figure 4.5. Average abundance of collembola and hexapoda in microhabitats (n=50) within two-age stands by year (1998-2000) at Wine Spring Creek watershed, N.C.



a) Oribatida
b) Immature Oribatida

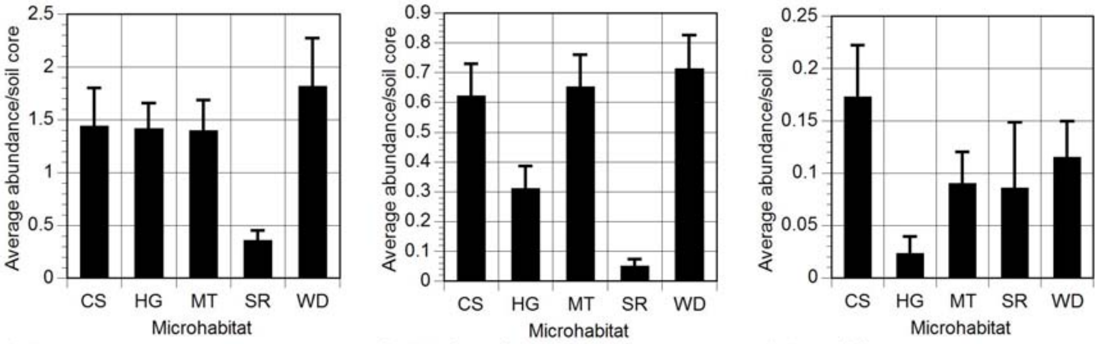


c) Mesostigmata
d) Pseudoscorpiones



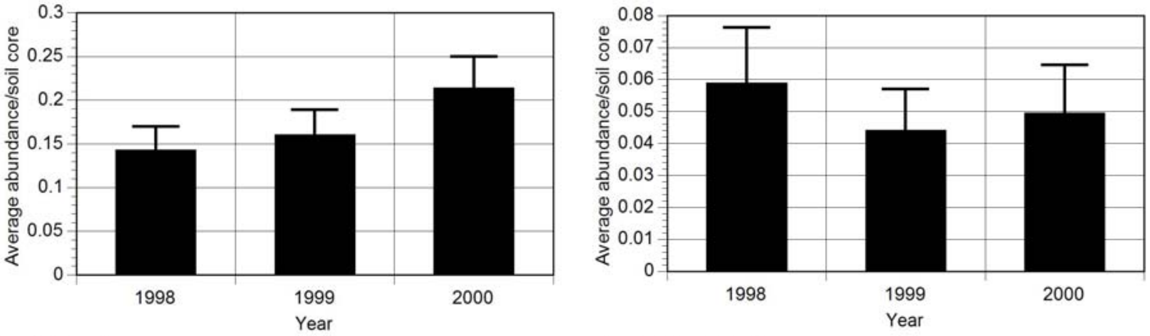
e) Prostigmata (with dominant subgroup)
f) Prostigmata (without dominant subgroup)

Figure 4.6. Abundance of soil microarthropods within microhabitats (n=150) in two-age cuts (1998-2000) at Wine Spring Creek watershed, N.C.



a) Proturans b) Myriapoda c) Araneida

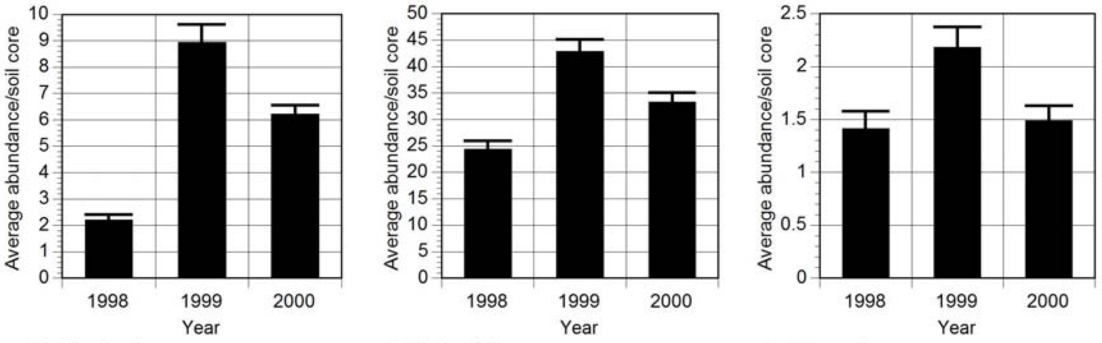
Figure 4.7. Abundance of proturans, myriapoda, and spiders within microhabitats (n=150) in two-age cuts (1998-2000) in Wine Spring Creek watershed, N.C.



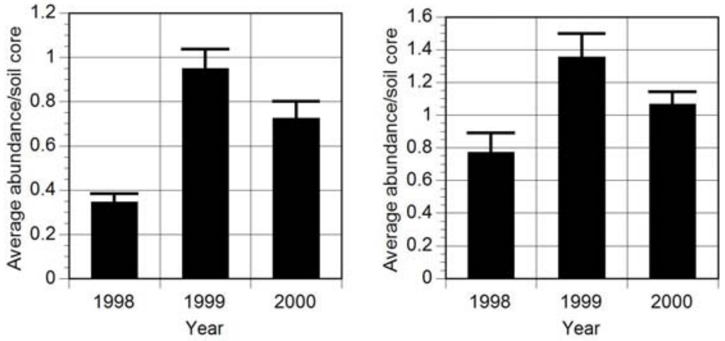
a) Araneida

b) Pseudoscorpiones

Figure 4.8. Differences in abundance of spiders and pseudoscorpions (n=250/year) among years (1998-2000) at Wine Spring Creek watershed, N.C.

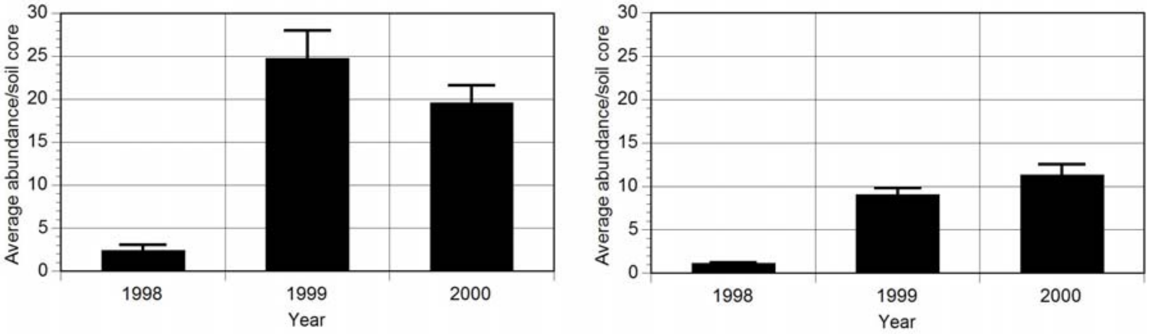


a) Collembola b) Oribatida c) Mesostigmata



d) Myriapoda e) Hexapoda

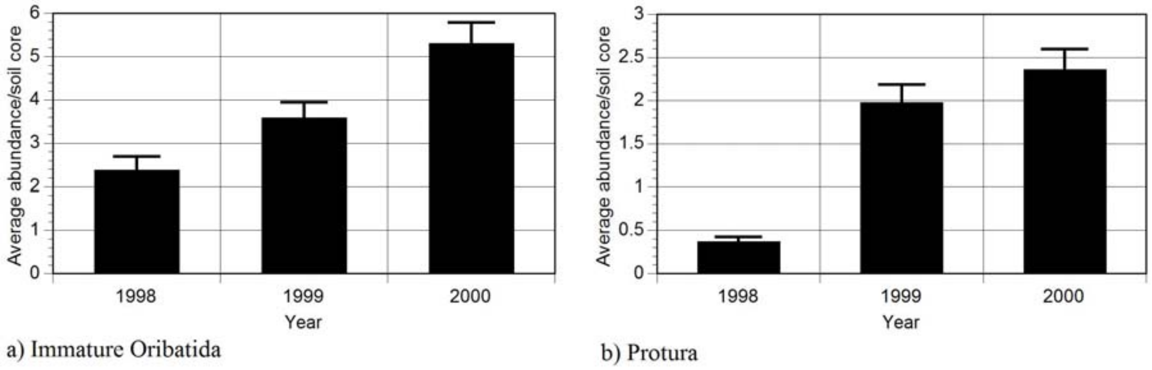
Figure 4.9. Differences in abundance of soil microarthropods (n=250/year) among years (1998-2000) at Wine Spring Creek watershed, N.C.



a) Prostigmata (with dominant subgroup)

b) Prostigmata (without dominant subgroup)

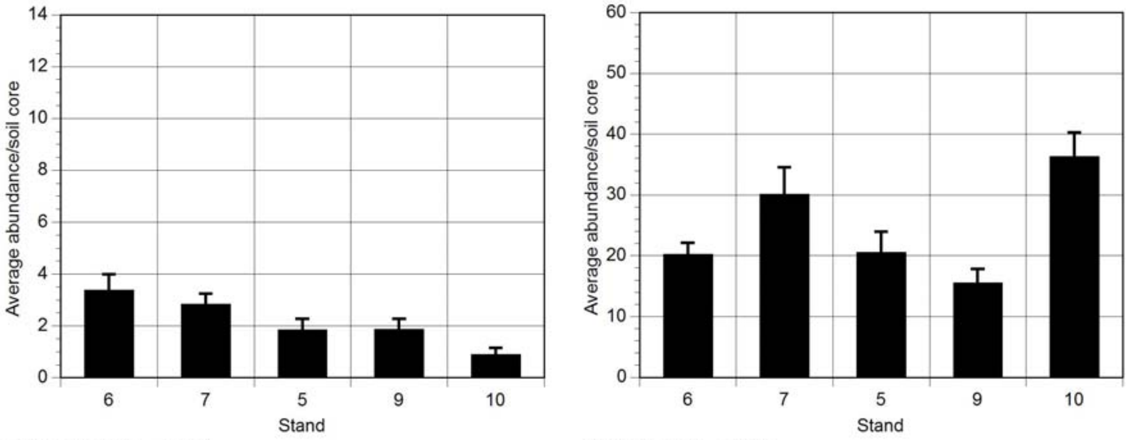
Figure 4.10. Differences in abundance of prostigmata with and without the dominant subgroup (n=250/year) among years (1998-2000) at Wine Spring Creek watershed, N.C.



a) Immature Oribatida

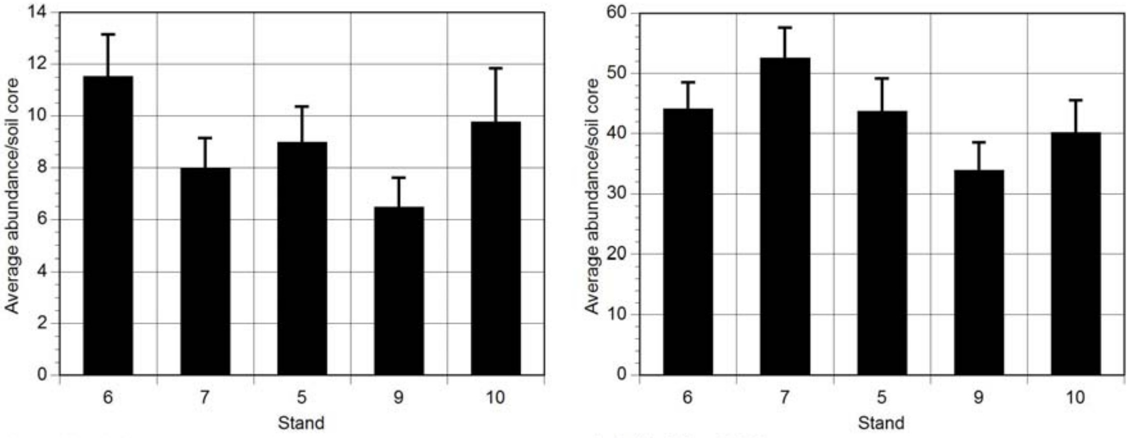
b) Protura

Figure 4.11. Differences in abundance of immature oribatids and proturans (n=250) among years (1998-2000) at Wine Spring Creek watershed, N.C.



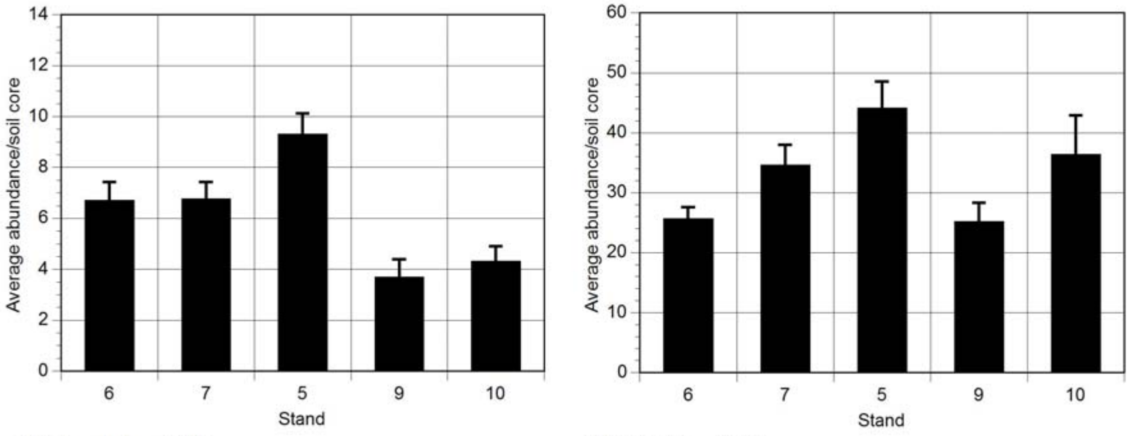
a) Collembola - 1998

d) Oribatida - 1998



b) Collembola - 1999

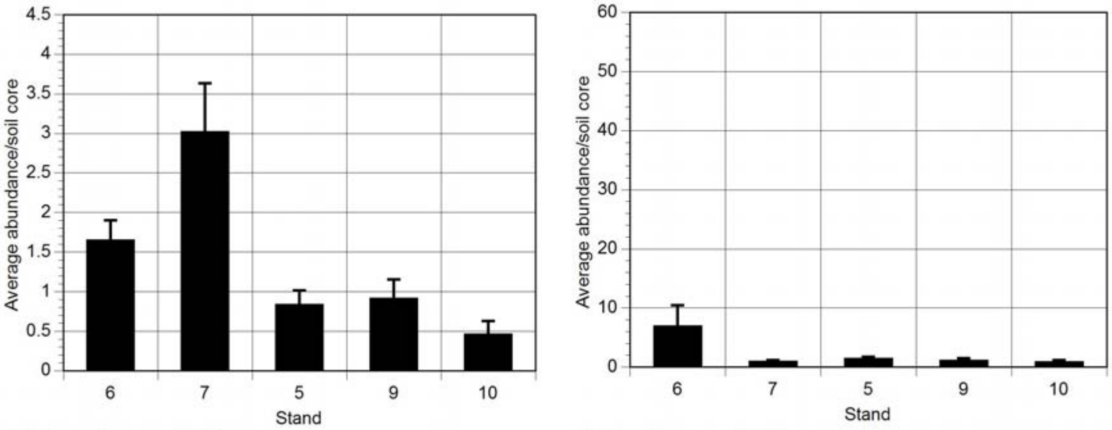
e) Oribatida - 1999



c) Collembola - 2000

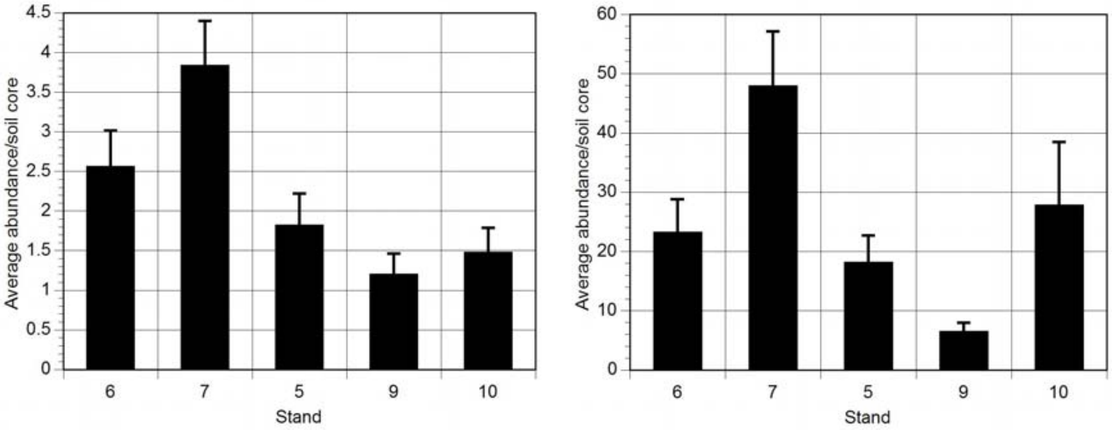
f) Oribatida - 2000

Figure 4.12. Differences in collembola and oribatid abundance in stands (n=50/stand) among years (1998-2000) at Wine Spring Creek watershed, N.C. (Controls: 6-7, Two-age: 5, 9, 10).



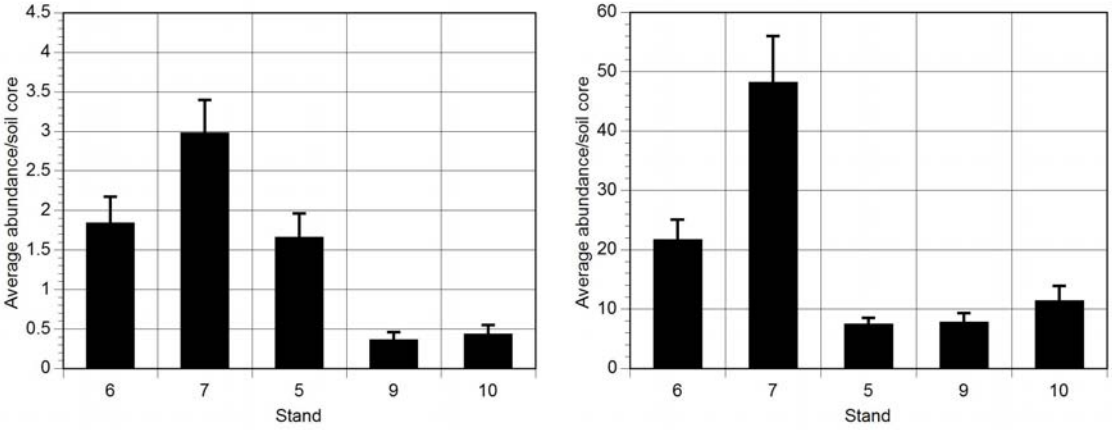
a) Mesostigmata - 1998

d) Prostigmata - 1998



b) Mesostigmata - 1999

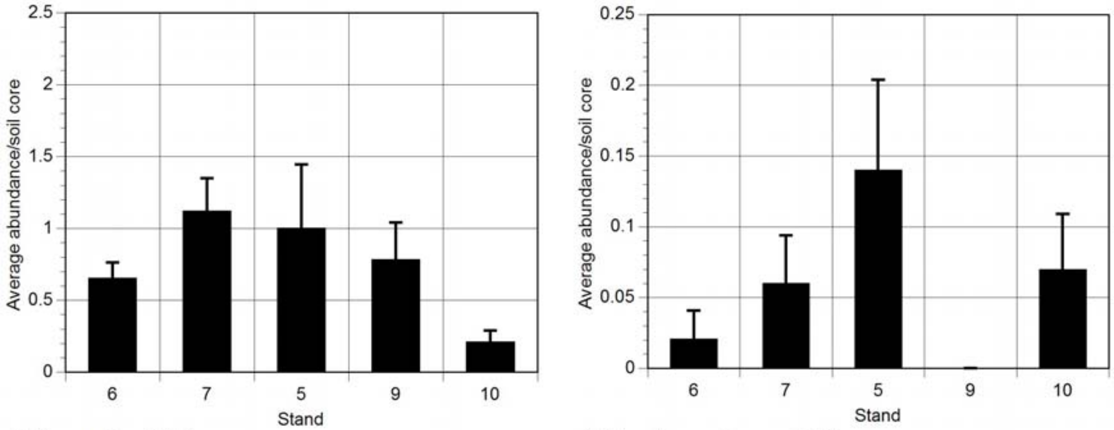
e) Prostigmata - 1999



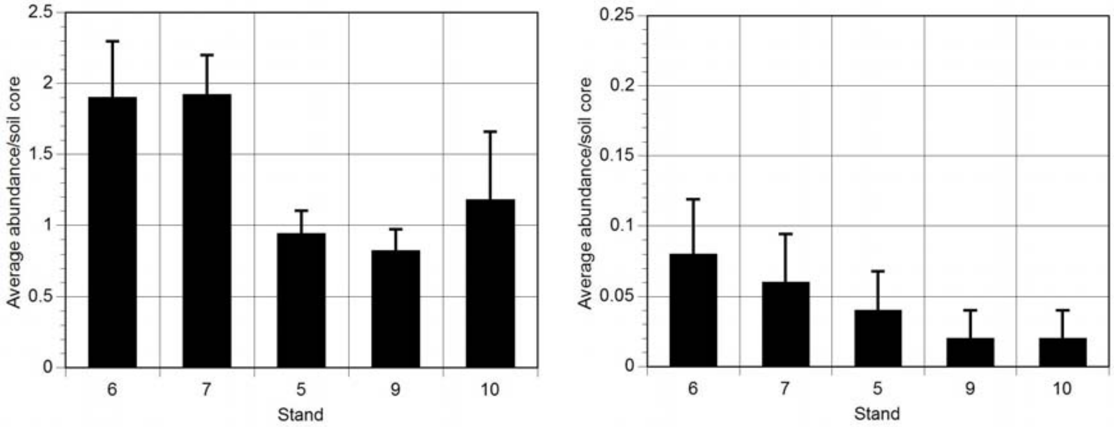
c) Mesostigmata - 2000

f) Prostigmata - 2000

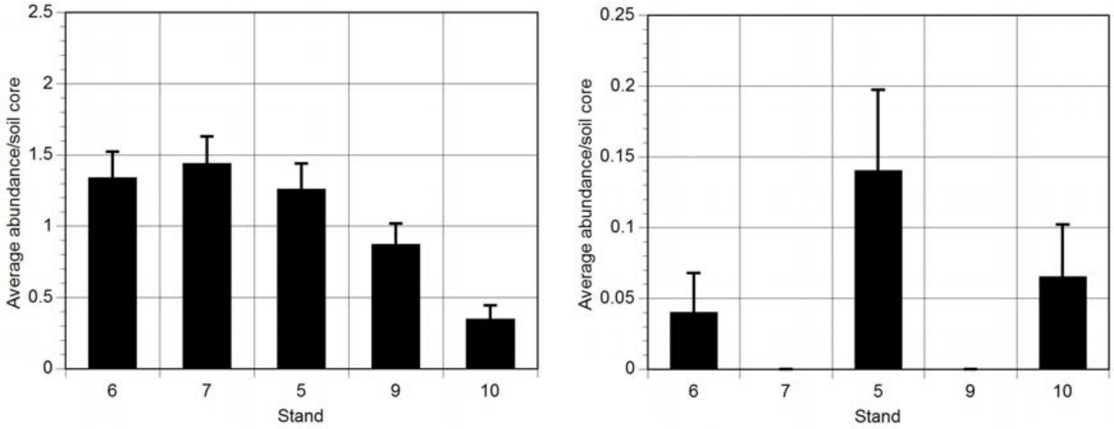
Figure. 4.13. Differences in abundance of mesostigmata and prostigmata in stands (n=50/stand) among years (1998-2000) at Wine Spring Creek watershed, N.C. (Controls: 6-7, Two-age: 5, 9, 10).



a) Hexapoda - 1998 d) Pseudoscorpiones - 1998

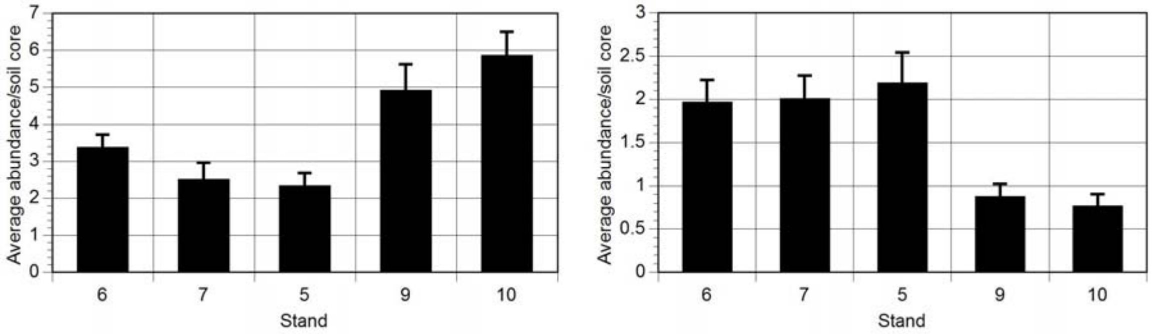


b) Hexapoda - 1999 e) Pseudoscorpiones - 1999



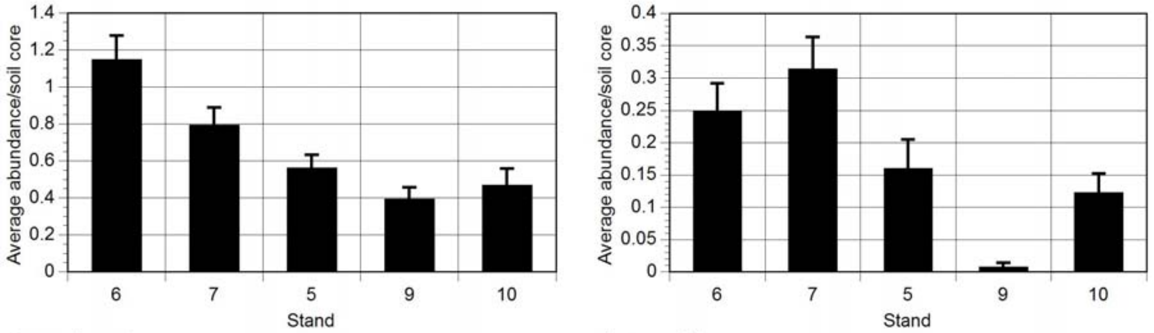
c) Hexapoda - 2000 f) Pseudoscorpiones - 2000

Figure 4.14. Differences in abundance of insects (a-c) and pseudoscorpions (d-f) in stands (n=50/stand) among years (1998-2000) at Wine Spring Creek watershed, N.C. (Controls: 6-7, Two-age: 5, 9, 10).



a) Immature Oribatida

b) Proturans



c) Myriapoda

d) Araneida

Figure 4.15. Differences in abundance of immature oribatids, proturans, myriapoda, and spiders in stands (n=50/stand), 1998-2000, at Wine Spring Creek watershed, N.C. (Controls: 6-7, Two-age: 5, 9, 10).

CHAPTER 5

CONCLUSIONS

The goal of this dissertation was to examine the response of soil microarthropod communities to two-age regeneration in the southern Appalachians. The effect of two-age regeneration on microclimatic conditions within stands was also investigated for the purpose of correlating macroscale landscape patterns (treatment effects) to microsite dynamics (soil arthropod communities).

Two-age regeneration altered microclimatic conditions across the landscape towards significantly greater fluctuations in soil temperatures, higher soil temperatures in summer months, cooler soil temperatures in winter months, decreased litter depth, and a trend towards decreased soil water content.

Soil temperatures within microhabitats varied significantly in the degree of fluctuation in daily temperature. Soil water content and bulk density were not significantly different among microhabitats, but litter depth varied significantly among microhabitats, suggesting that litter depth was a primary driver of differences in the community composition of soil organisms. The relatively rapid and high accumulation of litter and organic material in the woody debris microhabitat reinforces the importance of retaining harvesting residues on site, in addition to their role in the gradual accumulation of organic matter, and as large-scale habitat structure and complexity within a stand. The effect of two-age regeneration on abiotic conditions such as soil temperature, soil water content, and organic matter accumulation across the landscape implies the potential for corresponding changes in decomposition rates, microbial communities, rates of nutrient cycling, seedling germination, vegetation and organism communities.

There is high natural spatial heterogeneity in microarthropod communities located five meters or further apart in hardwood stands in the southern Appalachians. While local soil temperature, moisture, litter quality and quantity may determine community dynamics over short distances (<1m), the weak spatial correlation seen to occur at 10-12 meters in this study may be the contribution of larger habitat structures, influencing areas greater than one meter square such as coarse woody debris and vegetation patches, to community dynamics. The variation of this result in time and space suggests that local processes, such as litter availability, quality, and decomposition rate, remain the stronger determinants of microarthropod community dynamics.

Two-age regeneration treatments did significantly decrease the abundance of most soil taxa, with the exception of the oribatids and immature oribatids. The increase in immature oribatids may reflect the availability of additional food resources and habitat niches to adult oribatids that are usually occupied by other functionally-similar soil taxa, such as the collembola. It may also reflect a release from predation as the soil arthropod predator functional groups, such as the mesostigmata, centipedes, and spiders, all showed decreases in abundance.

The abundance of soil taxa varied among microhabitats within the harvested stands. The most likely explanation for differences in microarthropod abundance among microhabitats is differences in microclimatic conditions. Degree of fluctuation in soil temperature, bulk density, and litter depth were significantly different among microhabitats.

Microhabitats can serve as a common scale for understanding more specifically the response of soil microarthropods to forest harvesting. Differences in microclimatic conditions within microhabitats are most likely responsible for differences seen in species composition and abundance among microhabitats. Decreases in microarthropod abundance are related to disturbance intensity. Assessment of the pattern and frequency of microhabitats within disturbed stands may serve as a means of assessing the response of the soil arthropod communities to disturbance.

North American forests have evolved through time to be resistant to chronic, even catastrophic, disturbances. Combining multiple silvicultural practices to create a mosaic of habitats, age-classes, and structures, without excess in any one practice, will allow forest managers to maintain ecosystem processes, maximum biological diversity, and to maximize public use of forest lands.