

RESPONSE OF FOREST FLOOR MICROARTHROPODS TO A FOREST REGENERATION BURN AT WINE SPRING WATERSHED (SOUTHERN APPALACHIANS)

by

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Abstract: We sampled microarthropods in litter and soil of the Wine Spring watershed on April 2, 1995 before the watershed was burned, again on May 9, 1995 immediately following burning, and two years later on June 9, 1997. Pre-burn samples revealed a high abundance of mites (Arachnida: Acari) and collembolans (Insecta: Collembola). Oribatid (Acari: Oribatei) mites were numerous and species-rich. Overall, 112 species of oribatids were identified. The fauna was similar to that described for watersheds at the Coweeta Hydrologic Laboratory, North Carolina, though some additional species not recorded for Coweeta were found at Wine Spring. Groups of microarthropods responded differently to the burning treatment. Prostigmata (Acari), mostly small and delicate forms, were initially reduced to less than 50% of their pre-burn numbers, but recovered after two years. Mesostigmata (Acari) mostly survived the immediate burn but were reduced two years later. Most species of oribatids survived the initial effects of the burn, but numbers were reduced by 55% and species richness by 20%. Over the following two years, the oribatid fauna continued to decline to 28% of pre-burn abundance and 70% of pre-burn species richness. The mosaic nature of the burn left refugia from which microarthropods may re-invade heavily burned areas, once litter layers become restored.

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Introduction

Soil microarthropods, particularly the mites (Arachnida: **Acari**) and collembolans (**Insecta**: Collembola) are hyperdiverse **taxa** with local assemblages composed of hundreds of species (Asquith et al. 1990). Their activity is an important determinant of organic litter decomposition and nutrient **mineralization** rates (Swift et al. 1979). Estimates of their contribution to mass loss by deciduous leaf litter range **from** 4% to 43% (Seastedt 1984). They act primarily by breaking up substrates, by 'stimulating microbial **decomposers**, and by grazing on microbial growth (Coleman and Crossley 1996, Lussenhop 1992).

The effects of forest management practices on soil microarthropods has been documented in several instances. Clear-cutting generally reduces populations of forest floor arthropods (**Huhta et al.** 1969, Bill et al. 1975, Seastedt and Crossley **1981**), and these reductions may persist for years **afterwards** (**Huhta et al.** 1969, Blair and Crossley 1988). Some of these reductions may be attributed to changes in microclimate (Seastedt and Crossley **1981**) or other physical factors. Following forest **fertilization** microarthropods may show population increases (**Weetman** and Hill 1973, Bailey 1994, Bird **1997**), although effects of fertilizers may be largely indirect.

Fire depresses microarthropod populations directly and indirectly through habitat destruction. Recovery 'of microarthropods **from** direct mortality. impacts will vary with **life** history, i.e.; Collembola and some **Prostigmata** have greater intrinsic rates of increase than do oribatid mites. **Recovery from** habitat destruction will depend both on habitat regeneration and recolonization rate of the animals, Most studies of fire effects on soil microarthropods have been done following wildfires, which destroy much of the forest floor. In these instances microarthropod numbers are substantially reduced (Hill et al. 1975, Sgardelis and Margaris 1993, Paqum and Codere 1997). Fewer studies have dealt with prescribed burns. **Metz** and **Farrier** (1973) examined forest floors in loblolly pine (***Pinus taeda*** L.) stands subjected to periodic or **annual burns**. They found that numbers of microarthropods were depressed **in annual** burns but not in periodic ones. Immediately after burning, the number of animals was reduced drastically. Similar results were described for collembolan populations (**Metz** and **Dindal**

1975). Species diversity of collembolans in periodically burned plots was increased,

We examined the effects of a prescribed stand-replacement fire (Elliott et al. 1998) on soil **microarthropods**, comparing immediate (one month) responses and two-year responses to **burning**. We gave special attention to the oribatid mites (**Acari: Oribatei**), since that group contains a large number of species in **forest** soils of the southern Appalachians (**Lamoncha and Crossley 1998**). The oribatids are a species-rich group generally, and because of their slow life cycles, should be the slowest **group** to recover from **fire** damage.

Materials and Methods

The Wine Spring watershed is **located** in the Nantahala Mountains of the Southern Appalachians. A description of the site; the **burning regime** and the vegetation **responses** is given by Elliott et al. 1998 and Vose et al., 1998. Briefly, this study is part of an ecosystem **management** project **initiated** with the **objective of** using and/or developing ecologically based concepts, principles and technology to achieve desired resource conditions. A program of **microarthropod** sampling was designed to **measure pre-burn**, immediate post-burn, and **two-year** post-burn **abundance** of microarthropods. We **sampled** soil and **litter microarthropods** on **April 2, 1995** before the watershed was **burned**, on **May 9, 1995** immediately **after burning**, and **finally** on **June 9, 1997**. At each time, samples were taken from six sites on **the watershed**: two at the **base**, two mid-slope; and two at **the ridge** (see Table 1). At each site **15** soil-litter cores were taken at random: The cores were **aluminum** sleeves 5 cm dia by 5 **cm deep**. Arthropods were removed **from** the samples using a **modified** micro-Tullgren extractor (Crossley and Blair 1991). Samples were sorted, using a **20-X** binocular **stereomicroscope**, and separated into mite suborders, collembolans, and other arthropods. Adult oribatid mites were identified to species.

Results

Fire Intensity at Sampling Sites

The intensity of **fire** varied among the sampling sites (Table 1). We had anticipated a gradient of degree of incineration, but instead the fire produced a mosaic of burned sites. The lowest site (A6) at the bottom of the watershed experienced little burn, judging **from** the percent of litter

incinerated. The most intense burn occurred at site B2, near the ridge. Generally, sites on the lower slopes and on the highest part of the ridge showed the smallest fire damage (Table 1). Our sampling sites represent but a **small** portion of the areas, and given the mosaic nature of the **stand** replacement **fire** (Vose et al. 1998), some variation is to be expected. The June, 1997 microarthropod samples contained **significant** amounts of charcoal in the litter layers (Table 1), corresponding **approximately** to the 1995 estimates of burn intensities in our particular sampling sites and thus supporting our earlier estimates.

Microarthropod Abundance

Total microarthropod populations revealed by our sampling were not **unusual** for the **southern Appalachian Region**, but declined **in** the **two** post-burn periods (Table 2). **Pre-burn** populations of some **200 microarthropods** per sample indicate 100,000 per **m²**. Similar estimates (93,000 per **m²**) were obtained for a south-facing watershed (**WS 2**) at **the nearby Coweeta Hydrologic Laboratory** (Seastedt and Crossley 1981). **Lamoncha and Crossley** (1998) reported an average of 65,000 **microarthropods** per **m²** along an elevation gradient at **Coweeta**. In the immediate post-burn period at **Wine Spring (May, 1995)** total microarthropod **numbers declined to about half of** the pre-burn **population** sizes. Two years-later, total populations **had declined still further** (Table 2).

Before the fire, abundance of the microarthropod groups did not vary **significantly** as a function of **elevation** on the slope. Similarly, microarthropod abundance **was not found to vary with elevation** at the **Coweeta Hydrologic Laboratory** (**Lamoncha and Crossley** 1998). In the immediate post-burn period (May 1995) most **microarthropod** groups were

Table 1. **Location** of sites for microarthropod samples and estimates of percent burned, Wine. **Spring** Watershed, 1995-1997. Arranged **from** highest (**B1**) to lowest (A6) sites.

Site Number	Position on Watershed	Percent Litter Incinerated (visual estimate, May, 1995)	*Charcoal Index (June, 1997)
B1	Ridge'	50%	1.3
B2	Ridge	100%	2.1
B3	Mid-slope	100%	2.4
B4	Mid-slope	75%	2.3
A5	Lower slope	30%	1.5
A6	Lower Slope	None	0.9

*Scale of 0 (no charcoal) to 3 (dominated by charcoal)

depressed (Table 2). Collembolan populations decreased in the mid-slope sites, but increased their numbers above pre-burn population sizes in the lower sites and at the ridge top site, so that average densities post-burn did not differ from pre-burn densities. Collembolans are capable of rapid reproduction (Hopkin 1997) and are able to respond rapidly to disturbances. In South Carolina, frequent or periodic prescribed burns were found to decrease collembolan abundance (Metz and Dindal 1975). Prostigmatic mites exhibited the greatest population declines, to an average of about 25% of pre-burn populations (Table 3). These mites are soft-bodied, delicate fungal feeders or tiny predators, and seemingly highly susceptible to fire on the forest floor. Average densities of the more robust Mesostigmatic mites,

mostly **predaceous** species in these samples, appeared to decline in post-burn samples, but the difference was not statistically significant ($P = 0.10$). **Total** abundance of oribatid mites declined about 55% (Table 3). Most adult oribatids are heavily **sclerotized**. Immature oribatids are not, but they did not suffer greater mortality than the adults.

Two years **after** the **fire** (June 1997) microarthropod populations again showed a **differential** response (Tables 2 and 3). Prostigmatic mites had rebounded to pre-burn population sizes. Mesostigmatic mites, oribatid mites and collembolans had reduced numbers generally. Abundance of mesostigmatic mites was less than 30% of pre-burn numbers, **oribatids less than 30%**, and collembolans about 60%.

Oribatid Mite Diversity

The southern Appalachian forested ecosystems support a large **number** of oribatid mite species (Hansen 1997; Lamoncha and Crossley 1998). In 90 pre-burn samples **from** the Wine Spring watershed we identified a total of 112 oribatid species. One month post-burn we found 90 species; two years later, 78 species. As is usual for **soil** microarthropods, these communities contain a few common species and many rare ones **represented** by a few individuals. **In** pre-burn samples all sampling sites on the watershed contained **similar** numbers of species (Table 4). Numbers of species were reduced in the immediate post-burn period, **from** a mean of 65 per site to 48.5 per site. Two years later there was a further reduction in the number of oribatid species to 34.8 per site. **Margalef's** Index, a measure of species richness, also declined following the burn (Table 4). Endophagous oribatid mites were especially decimated by the burn. These species are obligate burrowers in woody substrates (woody **debris**, **petioles**, twigs, needles) as juveniles, and **are** thus dependent upon the presence of woody microhabitats. They tend **towards** larger body sizes and, most **likely**, slower life cycles: They are also functionally distinct from most microarthropods in their direct role in the degradation of substrates (**Bal 1970**, Hansen 1997). After two years endophages in the ridge and slope sites (sites B1 - B4) had **declined** to '10% of the pre-burn samples, whereas the lower, essentially **unburned site** A6 retained 78% of the endophagous oribatids.

Table 2. Abundance of mites and collembolans in samples taken pre-burn, one month post-burn and two years post-burn periods, Wine Spring watershed; 1995- 1997. Each number represents a mean of fifteen cores, 5 cm dia X 5 cm deep. Arranged from lowest (A6) to highest (B2) fire intensity.

Site Number	Prostigmata	Mesostigmata	Oribatei	Collembola	Total
Preburn					
A6	37.7	15.8	103.4	25.1	182.0
A5	65.3	26.9	125.2	28.0	245.4
B1	26.6	11.9	106.1	24.9	169.5
B4	34.8	25.3	112.5	47.0	219.6
B3	46.5	22.6	77.0	38.2	184.3
B2	34.9	13.5	96.7	11.0	156.1
mean	41.0	19.3	103.5	29.0	192.8
S.E.	±5.52	±2.62	±6.60	±5.05	rt13.56
One Month Post-burn					
A6	8.4	15.9	77.0	40.3	141.6
A5	18.7	23.1	79.2	37.6	158.6
B1	13.1	10.4	48.7	32.1	104.3
B4	12.1	12.5	41.7	40.2	106.5
B3	6.9	8.7	54.3	18.1	88.0
B2	3.6	12.5	52.3	8.5	76.9
mean	10.5	f3.8	58.9	29.5	112.6
S.E.	±2.17	±2.10	k6.33	±5.40	zk12.83
Two Years Post-burn					
A6	37.3	7.2	46.3	18.1	108.9
A5	69.0	7.9	43.2	18.2	138.3
B1	16.1	5.2	17.3	11.0	49.6
B4	37.8	6.3	22.3	14.7	81.1
B3	18.5	5.2	16.5	15.6	55.8
B2	58.3	5.2	27.6	12.7	103.8
mean	39.50	6.17	28.8	15.05	89.58
S.E.	±8.60	k0.48	f5.30	k1.18	f13.85

Table 3. Abundance of mites and **collembolans** in post-burn samples, as a percentage of pre-burn abundances. Arranged **from** lowest (A6) to highest (**B2**) fire intensity

Plot	Prostigmata	Mesostigmata	Oribatei	Collembola	Total
One Month Post-burn					
A6	22.3 %	100.6 %	74.5 %	160.6 %	77.8 %
A5	28.6 %	85.9 %	63.3 %	134.3 %	63.9 %
B1	49.3 %	87.4 %	45.9 %	128.9 %	61.5 %
B4	34.8 %	49.4 %	37.1 %	85.5 %	48.5 %
B3	14.8 %	38.5 %	56.1 %	47.4 %	47.7 %
B2	10.3 %	92.6 %	54.1 %	77.3 %	49.3 %
mean	26.7 %	75.7 %	55.2 %	105.7 %	58.1 %
S.E.	±5.78 %	±10.32 %	±5.31 %	±17.23 %	±4.85 %
Two Years Post-burn					
A6	98.8 %	45.6 %	44.8 %	72.1 %	59.8 %
A5	105.7 %	29.4 %	34.5 %	65.0 %	56.4 %
B1	60.5 %	43.7 %	16.3 %	44.2 %	29.3 %
B4	108.6 %	24.9 %	19.8 %	31.3 %	37.2 %
B3	39.8 %	23.0 %	21.4 %	40.8 %	30.3 %
B2	167.0 %	38.5 %	28.5 %	115.0 %	66.5 %
Mean	96.7 %	34.8 %	27.5 %	61.4 %	46.6 %
S.E.	±17.92 %	±3.96 %	±4.34 %	±12.37 %	±6.60 %

Table 4. Numbers of oribatid mite species in Wine Spring watershed sites before burning (April 1995), one month post-burn (May 1995) and two years post-burn (June 1997). Arranged from lowest (A1) to highest fire intensity (B2). Variates are species found in 15 samples at each site.

Site Number	Pre-Burn	One Month Post-Burn	Two Years Post-Burn
A 6	61	52	41
A 5	67	55	42
B1	70	46	31
B 4	61	44	30
B3	64	43	30
B 2	67	51	35
Mean (SE)	65 · 1.48	48.5 · 1.98	34.8 · 2.24
Total Individuals	09,310	5,202	4,699
*Margalef Richness Index	16.6	12.9	9.8

*S-1/log_e N. Based on numbers of adults only,

The dominant oribatid taxa remained essentially the same ones in pre-burn and post-burn periods. The species complex *Suctobelbella* and the widespread species *Oppiella nova* and *Tectocepheus velatus* were the most numerous of the taxa throughout the sampling period (Table 5). These same taxa are dominant in other southern Appalachian forest floors as well (Lamoncha 1994, Hansen 1997). Their habitat is the lower 0 layer and mineral soil, rather than the litter layer.

Discussion

Forest fires can have both direct and indirect effects on forest floor invertebrates. Initial heat may destroy populations of some fauna, and **long-term** effects on **faunal** habitats and resources may persist for years. Cutting of stands followed by intense fires can reduce the forest floor and decimate the soil **fauna**, with few survivors (Paquin and Coderre 1997). Critical **temperatures for** soil mites are around 30 - 32 °C, at which animals become inactive and subsequently desiccate (Wallwork 1960). Survivors of an intense burn of the forest floor are those species able to escape by migrating downward into the soil. A prescribed stand-replacement **fire** of the type investigated here will create a mosaic of burned and unburned areas (Vose et al. 1998). We observed that some of our burned sites (Table 1) **were** surrounded by **virtually** unburned forest floor. Unburned patches should serve both as **refugia from** which **fauna** can recolonize, and as a source of litter input that can begin to restore the litter habitat in adjacent burned areas. **In** the longer term, opening of forest canopies will increase insolation and decrease soil moisture. Soil microarthropods **tend** to increase their depth distribution under those conditions (Seastedt and Crossley 1981). With prescribed burning, litter layers **may** require decades to return to the original depth (Ffolliot and Guertin 1990), litter decomposition rates decline and microbial pools of nutrients may change (Monleon and Cromack 1996). Changes in litter quality may accompany changes in stand composition, if leaf fall consists of significant amounts of herbaceous vegetation or leaves of higher quality (lower **lignin** content). Our samples of soil microarthropods **from** the Wine Spring watershed revealed a rich, diverse community of species, resembling other studies in the southern Appalachians. Immediate effects of the prescription **fire** were seen as reductions in numbers of **microarthropods**. Given the short time between pre-burn and **post-burn** samples, we feel confident in attributing differences in microarthropod abundance to effects of the **fire**.

Table 5. Ranks of the **three most abundant oribatid** species in sites sampled at the Wine **Spring** watershed. Arranged **from** lowest (A6) to highest (**B2**) fire intensity.

Species	Site					
	B1	B2	B3	B4	A5	A6
	P r e - b u r n					
<i>Suctobelbella</i> spp.	1	2	1	2	1	2
<i>Oppiella nova</i>		1	2		1	2
<i>Tectocepheus velatus</i>	3	3	3			3
<i>Xylobates robustior</i>					3	
<i>Atropacarus stictulus</i>	2					
<i>Microppia minus</i>				3		
	One month post-burn					
<i>Suctobelbella</i> spp.	1	1	2	1	1	3
<i>Oppiella nova</i>	2	3	1	2	2	1
<i>Tectocepheus velatus</i>	3	2			3	2
<i>Ramusella</i> sp.				3		
<i>Ceratozetes mediocris</i>			3			
	One year post-burn					
<i>Suctobelbella</i> spp.	2	1	1	1	2	1
<i>Scheloribates</i> sp.	1	2	2			
<i>Tectocepheus velatus</i>	3	3			1	2
<i>Oribatula tibialis</i>			3			
<i>Brachychthonius jugatus</i>			2			
<i>Oppiella nova</i>				3	3	
<i>Lasiobelba rigida</i>						3

Unlike canopy arthropods, **soil mites** do not show rapid changes in pop& abn size. In research at the Coweeta Hydrologic Laboratory, Lamoncha and Crossley (1998) found no **difference** between soil **microarthropod abundance** in April and May, 1992. Large increases in collembolan populations **occurred** late winter to early spring in the southern Appalachians (Lamoncha and Crossley 1988; Crossley unpub.). No such increases were seen at Wine Spring, but **collembolans** either **recovered quickly** or were not suppressed by the fire (Table 2, 3).

Declines in microarthropod abundance ' **from** just post-burn to the census two years later indicates that habitat **degradation had long-term effects** on rates of mortality and reproduction. Many **cores taken after two years** contained a substantial amount of charcoal, upon **which little or no litter had** accumulated. Except for the Prostigmata, **which had** near complete **recovery** of overall abundance, all groups were **reduced**. **The majority of the Prostigmata** in the samples taken two years **post-burn were tiny members of** the Family **Nanorchestidae**. It is likely that **the burn is responsible for shifts** in abundance of species of Prostigmata. **The reductions in other** microarthropod groups seemed distributed across all sampling sites on the watershed. The small numbers of endophagous oribatids also suggest a significant change in community structure.

Microarthropod groups will vary in their ability to recover **from fires** such as this forest regeneration burn. Recovery will depend upon their **initial** sensitivity to the burn, their intrinsic rates of increase (**life history**), and their habitat requirements. Fundamentally, re-establishment of the **microarthropod** community will be determined by recovery **of** the habitat, although species with slow **life** cycles and low dispersal rates may lag behind habitat recovery. Initial survival was doubtless aided by the mosaic nature of the forest regeneration burn. Recovery should be aided by the closeness of colonizers, especially important for those species with low dispersal rates, and amelioration of burned patches by improving microclimate and providing leaf litter input.

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Literature Cited

- Asquith, A., J. D. Lattin and A. R. **Moldenke**. 1990. Arthropods: the invisible diversity. Northwest Environ. Jour. 6: **404-405**.
- Bailey, Michelle** Lynn. 1994. Soil microarthropods in pine plantations: effect of landscape system classification site **unit**, root **mat**, **litterfall**, moisture, and nutrient additions on abundance. MS Thesis, Univ. of Georgia. 121 p.
- Bal, L. 1970. **Morphological** investigation in two moder-humus profiles and the role of soil **fauna** in their genesis. Geoderma-4: **5-37**.
- Bird**, Simon. 1997. The effects of **silvicultural** practices on soil and leaf litter arthropods **in an East** Texas pine plantation. **Ph.D.** Dissertation, Texas A&M Univ. 193 p.
- Blair, J. M. and D. A. Crossley, Jr. 1988. Litter decomposition, nitrogen **dynamics** and litter microarthropods in a southern Appalachian hardwood forest 8 years following clear-cutting. Jour. **Appl. Ecol.** 25: 683-698.
- Coleman, D. C. and D. A. Crossley, Jr. 1996. Fundamentals of Soil Ecology. Academic Press, San Diego. 205 p.
- Crossley, D. A. Jr. and J. M. Blair. 1991. A high-efficiency, "low-technology" **Tullgren-type** extractor for soil microarthropods. Agric., Ecosys. and Environ. 34: 465-471.
- Elliott, K. J., R. L. **Hendrik**, A. E. Major, J. M. Vose and W. T. Swank. 1998. Vegetation dynamics following stand-replacement prescribed fire in the southern Appalachians. Forest. Ecol. **Manag.** (in press).
- Ffolliot, P. F. and D. P. **Guertin**. 1990. Prescribed **fire** in Arizona ponderosa pine forests: 24-year case study. pp. 250-253 *In*: J. S. **Krammes** (ed.)

- Proc.** Effect of Fire Management of Southwestern Natural Resources. USDA For. Serv. G-en. Tech. Rep. RM-191.
- Hansen, R. 1997. Effects of habitat heterogeneity and composition on the abundance, diversity and functional impact of the oribatid mite assemblage in leaf litter. Ph.D. Dissertation, Univ. of Georgia. 136 p.
- Hill, S. B., L. J. Metz and M. H. **Farrier**. 1975. 'Soil mesofauna and silvicultural practices. pp. 119-135 in B. **Bernier** and C. H. **Winget** (eds.) Forest Soils and Forest Land Management. Universit . Laval, Quebec.
- Hopkin**, S. P. 1997. The Biology of Springtails. **Insecta: Collembola. Oxford University Press, Oxford.**
- Huhta, V., M. Nurminen** and A. Valpas. 1969. Further notes on the **effect of** silvicultural practices upon the fauna of coniferous-forest soil. Ann. Zool. **Fenn.** 6: 327-334.
- Lamoncha, **K. L.** 1994. Spatial and temporal-variation in diversity of soil Oribatida in southeastern Appalachian forests. MS Thesis, **Univ. of Georgia.** 212 p.
- Lamoncha, **K. L.** and D. A. Crossley, Jr. 1998. Oriiatid mite diversity along an elevation gradient in a southeastern Appalachian forest. **Pedobiol.**
- Lussenhop**, J. 1992. Mechanisms of microarthropod-microbial interactions 'in soil. Adv. Ecol. Res. 23: **1-33.**
- Metz. L. J. and D. L. Dindal. 1975. Collembola populations and prescribed burning. Environ. Ent. 4: 583-587.
- Metz, L. J. and M. H. **Farrier**. 1973. Prescribed burning and populations of soil mesofauna. Environ. Ent. 2: **433-440.**

Monleon, V. J. and K. Cromack, Jr. 1996. **Long-term** effects of prescribed underburning on litter decomposition and **nutrient** release in ponderosa pine stands in central **Oregon**. **For. Ecol. Manag.** **81**: 143-152.

Paquin, P. and **D. Coderre**. 1997. Deforestation and **fire** impact on edaphic **insect larvae** and other macroarthropods. **Environ. Ent.** **26**: 21-30.

Seastedt, T. R. 1984. The **role** of **microarthropods** in decomposition and **mineralization** processes. *Ann. Rev. Entomol.* **29**: **25-46**.

Seastedt, T. R. and D. A. Crossley, Jr. 1981. Microarthropod response following cable logging and clear-cutting in the southern Appalachians. *Ecology* **62**: **126-135**.

Sgardelis, S. P. and **N. S. Margaris**. 1993. Effects of **fire** on soil **microarthropods** of a **phryganic** ecosystem. **Pedobiol.** **37**: 83-94.

Swift, M. J., O. W. Heal and J. M. Anderson: 1979. Decomposition in Terrestrial Ecosystems. Univ. **California** Press, Berkeley. 372 p.

Vose, J. M., W. T. Swank, B. D. Clinton, J. D. Knoepp and L. W. Swift, Jr. 1998. **Restoring** southern Appalachian **pine/hardwood** ecosystems with fire: a comparison of two techniques. *For. Ecol. Manag.*

Wallwork, John A. 1960. Observations on the **behaviour** of some oribatid mites in experimentally-controlled temperature gradients. **Proc. Zool Soc.** London **135**: 619-629

Weetman, G. F. and S. B. Hill. 1973. General environmental and biological concerns in relation to forest fertilization. *in* A. L. Leaf and R. E. Leonard (eds.) **Forest Fertilization Symposium** Proceedings. USDA For. Serv. Gen. Tech. Rep. NE-3. 246 p.