Department of Forest Science
Oregon State University
Corvallis, Oregon 97331-5704 (503) 754-2244

September 12, 1984

Dear :

Enclosed please find a plan for an experimental study on termites, wood decomposition and nutrients, which is being proposed by Walter G. Whitford for funding by the LTER Coordinating Committee. Please review the proposed study and send your comments to me as soon as possible, as the work is being proposed for October 1984.

Thank you for your prompt response to this request.

Sincerely,

JERRY F. FRANKLIN
Project Leader, RWU-1251

/JBrenneman/420-4361/09/10/84--Doc.ID # 0348F

Approved by phone (9-17-84) by Jerry.

COLLEGE OF ARTS AND SCIENCES

DEPARTMENT OF BIOLOGY
Box 3AF/Las Cruces, New Mexico 88003
Telephone (505) 646-3611

NEW MEXICO STATE UNIVERSITY ®

14 August 1984

Dr. Jerry Franklin
Forestry Sciences Laboratory
3200 Jefferson
Corvallis, OR 97331

Dear Jerry,

At the AIBS meeting Liz Blood and I talked at some length about setting up an experimental study on termites, wood decomposition and nutrients at the North Inlet upland site. The data to be collected will be contrasted and compared with the desert wood decomposition study at Jornada and provide data for comparisons of coastal plain forest (pine plantations) with the Andrews coniferous Forest. I enclose a brief outline of the experiment we hope to set up.

We request funds for me to travel to South Carolina to make some field estimates of termite populations and to set up the study. The Jornada group will be doing the wood fauna studies and the chemistry will be done at Univ. of South Carolina.

We plan on setting up this experiment in October 1984. I will be on the east coast during that time so would need travel support from Providence to Charleston, S.C. and per diem for six days. The round trip air fair is $520.00 and six days per diem is around $360.00. I am requesting $880.00 for this project.

Sincerely,

Walt

Walter G. Whitford
Professor

WGW/bcm

Enclosure

Experiment:
The role of termites in wood decomposition in a coastal plain forest.

The objective is to evaluate the role of termites in decomposition of pine logs and to obtain data on wood decomposition rates, nutrient immobilization in dead logs and nutrient release during decomposition.

We will place 50 cm log segments of diameter 10 - 15 cm on the mineral soil. Each log segment will be tagged with a number and original drymass. We will utilize a series of small plots with logs evenly spaced on the graded plots. One half of the plots will be assigned at random for termite exclusion. We will soak a 1 m2 area of soil under each log with a 1% chlordane solution to exclude termites. The logs will be exposed to other wood boring insects and other decomposer organisms. We will retrieve samples at 3 mos., 6 mos., 9 mos., 1 year, 1.5 years, 2 years and 2.5 years. We will remove 15 log segments from each treatment. When the segments are collected, they will be shipped to Las Cruces for extraction of insects, evaluation of fungal invasion along termite tunnels, etc. The logs will then be homogenized and ground samples will be sent back to S.C. for cation analysis. Nitrogen analysis will be done in Las Cruces.

While in S.C. in October 1984, I will conduct a quantitative survey of the occurrance of termites at the North Inlet site using plotless techniques as described in Gentry and Whitford 1982 (see attached reprint). I should be able to complete collection of the baseline data on termite populations and other wood boring arthropods during a 5 day stay at North Inlet.

UNIVERSITY OF GEORGIA
INSTITUTE OF ECOLOGY
ATHENS, GEORGIA 30602 TELEPHONE 542-2968

September 18, 1984

Dr. Jerry Franklin
Department of Forest Science
Oregon State University
Corvallis, OR 97331-5704

Dear Jerry:

I heartily endorse the wood decomposition experiment proposal by Whitford and Blood.

Perhaps Whitford's plans include attending the Coweeta Symposium in October, since he will be near here. If he could do so, for a small additional amount of money, we could explore duplicating the experiment at Coweeta and at the Okefenokee.

Sincerely yours,

D. A. Crossley, Jr.
Professor

DAC/pc

UNIVERSITY OF COLORADO, BOULDER

Niwot Ridge/Green Lakes Valley
Long-Term, Ecological Research (LTER)

19 September 1984

Dr. Jerry F. Franklin
Project Leader, RWU-1251
Oregon State University
Department of Forest Science
Corvallis, OR 97331-5704

Dear Jerry:

Here is my response to Walt Whitford's proposal to examine termites and wood decomposition. Since Walt is the recognized expert on termites, and I am supportive of inter-site comparisions, and since the request of $880 is modest, I strongly support the proposal and I recommend that it be funded, if funds permit, from the LTER Coordinating Committee grant.

Yours sincerely,

Pat

Patrick J. Webber
Principal Investigator
Niwot Ridge LTER

PJW/rlp

Institute of Arctic and Alpine Research • Campus Box 450 • Boulder, Colorado 80309 • (303) 492-6387

State Natural History Survey Division

ENR

Natural Resources Building
607 East Peabody Drive
Champaign, IL 61820
217/333-6880

Illinois Department of
Energy and Natural Resources

River Research Lab
Box 599
Havana, IL 62644
(309) 543-3950/3105

17 September 1984

Dr. Jerry Franklin
Department of Forest Science
Oregon State University
Corvallis, OR 97331-5704

Dear Jerry:

I approve Walt Whitford's request of $880.00 for an intersite study on termites, wood decomposition and nutrients. I assume from Walt's letter that the study is being done on three sites (North Inlet, Jornada, and Andrews), although the proposal mentions only North Inlet.

Sincerely,

Rip Sparks

Richard E. Sparks

RES:va

Judy file

UNIVERSITY OF SOUTH CAROLINA

COLUMBIA, S. C. 29208

BELLE W. BARUCH INSTITUTE FOR
MARINE BIOLOGY AND COASTAL RESEARCH

(803) 777-5288

October 1, 1984

Jerry F. Franklin
Department of Forest Science
Oregon State University
Corvallis, Oregon 97331-5704

Dear Jerry:

Sounds good to me. Liz is involved and I could not be anything but enthusiastic. A good intersite study.

Best wishes.

Sincerely yours,

F. John Vernberg (mts)

F. John Vernberg
Director

FJV:mts

The University of South Carolina: USC Aiken; USC Salkehatchie, Allendale; USC Beaufort; USC Columbia; Coastal Carolina College, Conway; USC Lancaster; USC Spartanburg; USC Sumter; USC Union; and the Military Campus.

Oecologia (Berl) (1982) 54:63–67

Oecologia

The Relationship Between Wood Litter Infall and Relative Abundance and Feeding Activity of Subterranean Termites *Reticulitermes spp.* in Three Southeastern Coastal Plain Habitats

J.B. Gentry and Walter G. Whitford*
Savannah River Ecology Laboratory, Drawer E, Aiken, SC 29801

Abstract.

We estimated the densities of termites in dead wood using a point-quarter technique in four habitats: pine plantations subject to control burning and unburned, lowland hardwood forest, and turkey oak woodland. The burned pine plantation had the highest estimated termite density, $13 \times 10^6 \cdot \mathrm{ha}^{-1}$ unburned pine plantation and lowland hardwood had estimated densities of $2.6 \times 10^6 \cdot \mathrm{ha}^{-1}$ and $2.2 \times 10^6 \cdot \mathrm{ha}^{-1}$, respectively, and the turkey oak woodland had an estimated densities of $61.9 \times 10^3 \cdot \mathrm{ha}^{-1}$. There were varying percentages of *Reticulitermes flavipes* and *R. virginicus* in the various habitats. There was nearly linear increase in percentage of pine blocks attacked by termites in the pine and hardwood forests and by the end of the growing season, nearly all had been channelized by termites. In the turkey oak habitat 70% of the pine blocks were channelized. Termites removed between 3% and 12% of the original mass of over one-fourth of the pine blocks during the growing season.

Wood litter in fall was highest in the lowland hardwood forest: $2869 \mathrm{~kg} \cdot \mathrm{ha}^{-1} \cdot \mathrm{yr}^{-1}$. Wood litter input in the long leaf pine plantation, $792 \mathrm{~kg} \cdot \mathrm{ha}^{-1} \cdot \mathrm{yr}^{-1}$ was nearly equivalent to the three year average wood litter in fall in a Danish oak forest.

Several recent studies have emphasized the importance of termites in wood decomposition (Kitchell et al. 1979; Ausmus 1977) and suggested that channelization by termites allows invasion of other arthropods, fungi, etc. thereby increasing the rate of wood decomposition (Kitchell et al. 1979). Other workers have attempted to estimate caste composition and relative densities of subterranean termites by placing bait bolts adjacent to logs containing known colonies of termites (Howard and Haverty 1981). Kitchell et al. (1979) suggested that termites may play an important role in nutrient cycling in forest systems. Despite these recent studies, little is known of the basic ecology of eastern forest subterranean termites.

We decided to undertake an ecological study of the role of termites in southeastern coastal plain ecosystems. Prior to establishing studies of the role of termites in nutrient turnover and energy flow, we felt it necessary to obtain some estimate of natural abundance of termites, characteristics of wood colonized, natural caste relationships, rates of location of potential food materials, rates of input of potential food material, and finally variation in attack rates of wood that may be a function of preconditioning by fungi or soil habitat type. Here we report the results of these studies.

Habitats

Our studies were conducted on four habitats on the Savannah River Plant Reserve approximately 40 km SE of Aiken, SC. Much of the Savannah River Plant has been planted in pine (*Pinus* spp.). Strips of native hardwoods referred to here as the lowland hardwood habitat line the river bottoms and are dominated by live oaks, *Quercus* Spp., sweet gum, *Liquidambar styraciflua* L. and tulip popular *Liriodendron tulipifera* L. In some of the ancient beach areas, the deep sand produces an edaphic semi-desert dominated by turkey oak, *Quercus nigra* L.; these areas are called turkey oak habitat.

These habitats are characteristic of the coastal plain from southern Virginia through northern Florida. The pine plantations provided an additional useful comparison in that one of the plantations had not been subjected to controlled burning or thinning (Reserve Plantation) while the other (Burned Plantation) had been subjected to controlled periodic burning and had been burned in late February.

Methods

With the exception of the turkey oak habitat, estimates of densities of foraging groups, characteristics of wood used, estimates of numbers, castes and species composition were made by the point-quarter method (Phillips 1959). This technique is commonly used to estimate densities of shrubs, trees, etc., and is amenable as a sampling technique for sedentary groups of organisms that may either be random or aggregated in dispersion. We selected a compass direction and random starting point then set all other points at 50 m intervals. At each point, a cross divided the surrounding areas into four imaginary 90° quadrants. From the center point of the cross, each quadrant was carefully searched until a segment of wood containing termites was encountered. The distance from the point to nearest termite group per quadrant was measured, and the length, diameter, wood species, proportion of the stem containing ter-

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0029-8549/82/0054/0063/$01.00

mites, and relative abundance of termites in the wood segment recorded. Twenty points were recorded in each of the pine habitats and the lowland hardwood area. In general it was impossible to identify the termites to species because of the absence of sexual forms.

The point-quarter technique was not applicable in the turkey oak habitat because of the sparcity of termite foraging groups. We randomly selected 10, 15 m radius circles and recorded all foraging groups found within that area and recorded the same data as in the point-quarter surveys.

From each habitat, termites were carefully removed from selected log segments, sorted and counted. Log segments were selected at random and were of the dominant species in that habitat. We examined a minimum of ten segments from each habitat. This provided estimates of numbers of termites per unit volume of wood. Termite densities were estimated by multiplying the number of termites per unit volume of wood by the average log volume in the habitat by the estimated density of logs in that habitat.

Comparisons of seasonal activity, attack rates and wood consumption in three habitats (excluding the burned pine habitat) were made by comparing bait block grids made of 2″ × 4″ × 10″ (5.08 cm × 5.08 cm × 10.16 cm *Pinus* spp. blocks). These grids were established between January 9 and January 29, 1979. Each grid was 30 blocks with 1 m block spacing. Control grids were placed in each habitat. The controls were blocks placed on soil which had been soaked with a 1% chlordane solution to prevent termites from attacking the blocks. In the lowland hardwood and turkey oak habitats, there was a fresh block grid and a preinoculated (aged by fungi) block grid in addition to the chlordane control blocks. The preinoculated blocks were cut from pine that had been exposed to the normal soil microflora for approximately one year. In the longleaf pine plantation, the block grids were identical to the other habitats plus an aged and fresh block grid placed on the surface of the pine straw rather than on the mineral soil.

Each grid was checked monthly. We recorded termite etching, number of termites persent, and if sufficient channelization had occured, those blocks were returned to the lab and dried to a constant weight for measurement of quantity of wood removed.

Wood infall was estimated by collecting all wood pieces larger that 2 cm in diameter. Five 20 m^2 plots in each habitat were cleared of all wood larger than 2 cm in diameter in April 1979. All new wood falling on these plots was collected each month, oven dried and weighed.

Results

The highest density (719 · ha^{-1}) of foraging groups of termites was in the lowland hardwood habitat. In the lowland hardwood habitat foraging groups were most frequently encountered in 2–6 cm diameter sticks (Table 1) and the relative abundance of termites per foraging group was lower than in the pine habitats. In the lowland hardwood habitat we estimated a density ($\bar{x} \pm$ SD) of 2,233, 341 ± 379,668 termites · ha^{-1} in comparison to the pine reserve plantation with 190 foraging groups · ha^{-1} and an estimated 2,585,040 ± 801,362 termites · ha^{-1}. The density of foraging groups in the burned pine plantation (469 · ha^{-1}) was double that of the pine reserve, but had an estimated density of 13,200,349 ± 4,224,111 termites · ha^{-1}. The turkey oak habitat had the lowest foraging group density 49.5 · ha^{-1}, with an estimated density of 61,957 ± 4,957 · ha^{-1}. In the lowland hard woods and pine plantations, nearly all old wood greater than 2 cm diameter had been previously used to some degree by termites. In the burned (managed) pine plantation, there were more large diameter logs and stumps colonized by termites than in the unmanaged pine reserve (Table 1). In the hardwood habitats, the termites appeared to prefer logs in a more advanced stage of decomposition than in pine habitats where class B and C logs most frequently supported termite colonies (Table 1).

Table 1. Comparisons of the numbers of logs in each diameter class and numbers of logs in each decay class with foraging groups of termites in them. Habitat abbreviations are: TO-turkey oak, LLHA-lowland hardwood, LLPB-longleaf pine burned, LLPR-longleaf pine reserve. Stumps containing termites were not assigned to diameter classes when most of the termite activity was below ground

	TO	LLHA	LLPB	LLPR
Diameter Class				
0– 2 cm	3	2	5	5
2– 6 cm	19	48	19	35
6–10 cm	1	9	19	20
10–20 cm	0	3	20	20
20 cm	0	4	16	0
Decay Class[a]				
A	0	3	1	0
B	12	18	21	30
C	5	23	43	31
D	15	17	3	7
E	3	16	9	12
F	0	3	3	0

[a] *A* – bark and cork cambrium intact; *B* – bark loose cork cambrium largely destroyed, wood solid; *C* – bark loose, wood punky; *D* – bark partly or completely missing, wood mostly decayed; *E* – heartwood only; *F* – almost humus

There were three distinct morphological species encountered. In the turkey oak habitat we found a morphospecies with small workers, but found no sexuals, therefore, we were unable to determine the taxon to which these termites should be assigned. In other habitats, we found varying percentages of *Reticulitermes flavipes* and *Reticulitermes virginicus*, respectively: lowland hardwood 26.6% and 73.4%, pine reserve 43.8% and 56.2% and burned longleaf pine 60% and 40%.

We collected log segments for termite counts in late February and March. In the pine branches in the Reserve Plantation, 16.7% of the logs contained larvae and 25% contained nymphs (unpigmented alates). Soldiers accounted for (N = 12) 4.6 ± 2.8% of the sampled populations. In the lowland hardwood samples (N = 17), 50% contained nymphs and 64.7% contained larvae. Soldiers accounted for 2.6 ± 1.7% of the sampeld populations in the lowland hardwood. In those logs with both nymphs and larvae, nymphs accounted for 8.5 ± 9.4% and larvae 11.7 ± 12.2% of the population. Soldiers made up a similar fraction of the foraging populations sampled from the pine-block baits 3.1 ± 3.4% (N = 36). The larger standard deviation is due to samples with no soldiers. Soldiers were rarely encountered when fewer that 25 workers were found in block or branch segments.

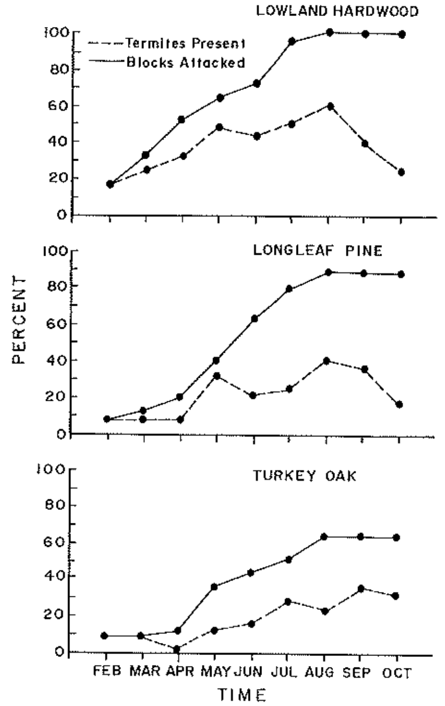

Fig. 1. Cumulative percentage of preconditioned pine blocks attacked by termites and percentage of blocks having termites present on each sampling date in the habitats indicated

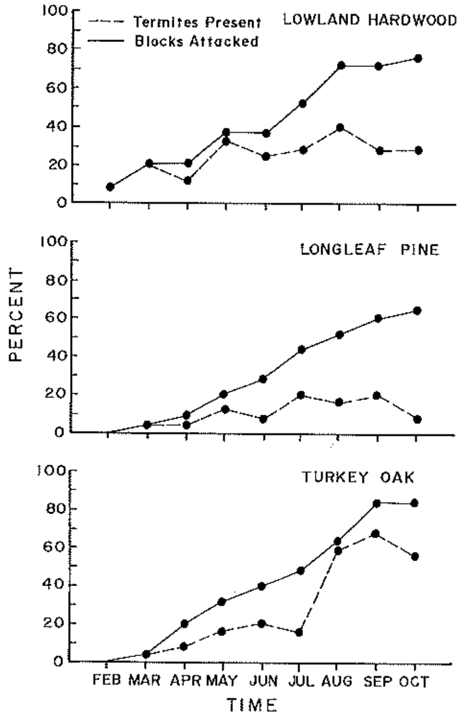

Fig. 2. Cumulative percentage of unconditioned pine blocks attacked by termites and percentage of blocks having termites present on each sampling date in the habitats indicated

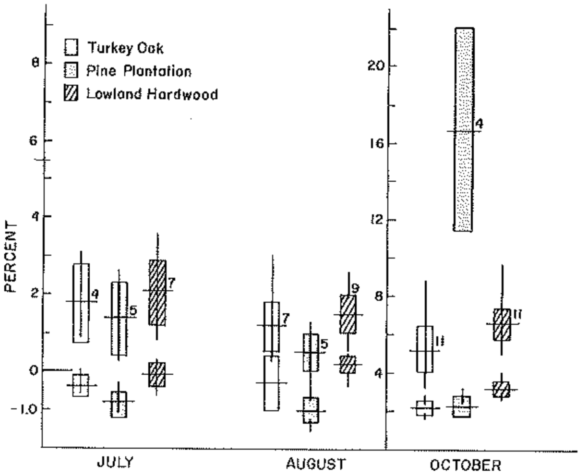

Fig. 3. Percent weight loss from pine blocks attacked by termites in comparison to percent weight change in blocks on Chlordane (TM) treated soil to eliminate termites. The rectangles equal ± 1 standard deviation. The horizontal line equals the mean and vertical line of the range. The number next to the mean equals the sample size

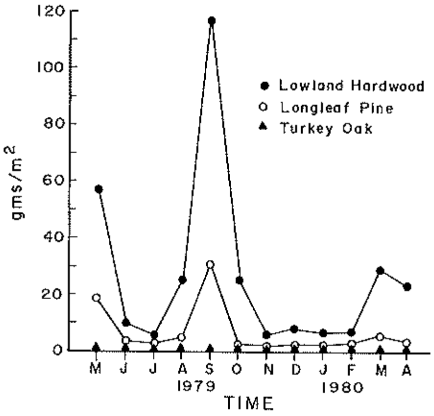

Fig. 4. Average monthly wood litter input in three forest habitats on the Savannah River Plant

There was a nearly linear increase in the number of precondition pine blocks attacked by termites in the lowland hardwood habitat and within eight months, all had been attacked (Fig. 1). In the longleaf pine area, the termites had attacked 90% of the preconditioned pine blocks on the mineral soil within 7 months but had attacked none of those placed on the surface of the pine straw. In the turkey oak area the cumulative number of preconditioned blocks attacked leveled off at 60% within 7 months (Fig. 1), and in the turkey oak habitat more blocks had termites present in September and October than the other habitats (Fig. 1).

Fewer of the unconditioned blocks were attacked and there were fewer unconditioned blocks with termites in the lowland hardwood and longleaf pine habitats (Figs. 1 and 2). However, in the turkey oak habitat, both cumulative numbers and numbers of blocks with termites present were higher in the unconditioned blocks than in the preconditioned blocks (Figs. 1 und 2).

In the first 6–7 months, termites consumed between 2% and 4% by weight of those blocks exhibiting sufficient channelization to warrant weighing (Fig. 3). After 9 months in the field, 20% of the blocks in the longleaf pine had lost 12–20% of the original weight attributed to termite feeding in comparison to 3–5% consumption loss to termites in 45% of the blocks in the turkey oak and lowland hardwood habitats (Fig. 3).

Wood infall was highest in the lowland hardwood habitat and was predominately small stems in the 2 cm–6 cm size class. The highest wood infall was coincident with high winds from hurricane David in September 1979 (Fig. 4). Strong spring winds also resulted in high wood input in both the longleaf pine and lowland hardwood habitats. There was consistently a low quantity of litter fall in the turkey oak habitat (Fig. 4) varying between ml $gm \cdot m^{-2}$ and 4.3 $gm \cdot m^{-2}$. Summing the wood infall for a year, we estimated 2,869 $kg \cdot ha^{-1} \cdot yr^{-1}$ in the lowland hardwood, 792 $\cdot kg \cdot ha^{-1} \cdot yr^{-1}$ in the longleaf plantation, and 117 $kg \cdot ha^{-1} \cdot yr^{-1}$ in the turkey oak habitat. In June-September 1980, we recorded 2,246 $kg \cdot ha^{-1} \cdot yr^{-1}$ in the lowland hardwood, 441 $kg \cdot ha^{-1}$ in the longleaf pine forest, and 88 $kg \cdot ha^{-1}$ in the turkey oak habitat.

Discussion

Lee and Butler (1977) report at least 9 species of termites occuring in a dry sclerophyll forest in Australia at total densities of between 1,000 and 1,500 m^{-2}.

In South Carolina, only the managed-burned pine plantation had estimated densities approaching those reported by Lee and Butler, but only *Reticulitermes* species occur in the South Carolina habitats. Any estimation technique which involves surface sampling of subterranean termites will underestimated numbers because the below-ground fraction is not sampled.

The turkey oak habitat was the least favorable for termites of the habitats examined. The low densities of termites in the turkey oak may be related to the availability of suitable foods. The turkey oak habitat is an edaphic desert. Tree density is low and the oaks are small and slow growing producing a dense wood. The oak habitat also lacks a closed canopy and the sandy soils dry quickly after rains. The distribution of dead stems and branches is very patchy in the turkey oak and most are smaller diameter which allows them to dry quickly.

However, the turkey oak attacked by termites was in the same stages of decomposition as wood in the other habitats which was attacked by termites. Dead oak (both standing and fallen) exhibited much less channelization. We also noted that pine stumps in the turkey oak area were completely hollowed by termites having the same appearance as pine stumps in the plantations. These features suggest that wood characteristics such as density and fiber composition affect the available energy source for termite populations, hence limiting the density of termites in the turkey oak habitat.

The lowland hardwood had the highest density of foraging groups and the highest frequency of foraging groups in small diameter stems. The lowland hardwood area also experienced the highest wood infall and most of that infall was smaller diameter stems. The densities of termites from a number of habitats was reviewed by Wood and Sands (1978). In the lowland hardwood habitat and unburned pine plantation habitat where estimated densities were approximately 250 $termites \cdot m^{-2}$ subterranean termite abundance was considerably lower than most forest estimates where densities exceeded $1{,}000 \cdot m^{-2}$ except in one South American rainforest study where numbers of one species were lower than estimated by our methods (Wiegert 1970). Only the burned pine plantation estimates approach those reported by Wood and Sands, 1978.

When termites locate small stems, these are rapidly channelized and the termites must move on to other food sources. Unfortunately, we have no data on comparative rates of mass loss from stems. In contrast, the pine plantations experience small diameter branch infall usually in the winter during ice storms and these branches lie on the surface of the pine straw, hence are unavailable to the termites. Input of large diameter dead wood occurs as stumps and logs during thinning and burning operations or when individual trees die. Standing dead pines in plantations were generally colonized by termites and channelization of the base weakens the bole thus decreasing the time the bole stands and increases the speed of wood turnover by termites. The fallen boles are quickly colonized and channelized. Controlled burning appears to enhance the availability of wood in the managed plantations by speeding the contact of dead wood with mineral soil. The block studies demonstrate that wood is not available to termites on the surface of pine straw accumulations, but that wood on the mineral soil is quickly attacked. The controlled burns remove pine straw and small wood, but do not harm the larger stems and tree holes.

The comparisons of pine bait blocks provide data on several behavioral characteristics of the *Reticulitermes spp.* There was consistently larger numbers of aged blocks attacked both on a seasonal and cumulative scale. This confirmed the well documented importance of preconditioning of wood by fungi prior to attack by termites, but this relationship did not hold in the turkey oak area, however, where there was actually greater attack on the new blocks in August–October and cumulatively more new blocks than preconditioned blocks were attacked. This may be due to the xeric edaphic nature of the turkey oak habitat and/or the activity of the *Reticulitermes* spp. in that habitat.

In all of the sub-populations of termites extracted from the log segments, we found a small percentage of soldiers (6.4%). A similar situation was reported for *Reticulitermes flavipes* by Howard and Haverty (1980). We found little variation in percentage of soldiers in colony segments with nymphs and larvae when compared to those with only workers. Unfortunately, like Howard and Haverty (1980), we are unable to offer any additional suggestions as to the reasons for variation in soldier percentages in *Reticulitermes* spp.

The comparisons of attack rates and weight losses by channelization demonstrate that subterranean termites are capable of rapid wood removal and are extremely important in wood decomposition in all of these habitats. The highest channelization losses occurred between August and October. Although the frequency of channelized blocks was lowest in the pine plantations, the weight losses were greatest. This may be due to different species foraging patterns in these habitats where the termites concentrate their efforts on a single food unit once it is discovered.

Wood litter infall in the lowland pine plantation was approximately the same as that in a Danish oak forest (Christensen 1978), but the wood infall in the lowland hardwood forest was considerably higher. Christensen (1978) discussed the importance of winds in producing variation in wood litter infall stating that the ratio of minimum wood litter fall averaged 1.6. In our study we recorded nearly as much wood litter infall in the longleaf hardwood in four months June–September 1980 as in the previous full year and this without the high input due to hurricane winds.

It is obvious that many factors affect quantity of wood input and as Lang and Foreman (1978) have pointed out, wood decomposition and mineralization can be very important in forest ecosystems.

Given the high densities, high rates of wood consumption and rapid colonization of wood by *Reticulitermes* in these southeastern forest ecosystems, in addition to the high rates of wood infall, it is probable that these insects play an important but as yet undocumented role in nutrient cycling in these systems.

Acknowledgements. Research was conducted under the auspices of contract EY-76-C-09-0819 between the U.S. Department of Energy and the University of Georgia. Linda Whitford and Michael Vargo assisted with the field work. W.G. Whitford was supported by a sabbatical leave from New Mexico State University, and a research participation agreement S-2020 from the Oak Ridge Associated Universities.

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Oecologia (Berl) (1982) 54:68–71

Oecologia

The Effects of Clipping and Fertilization on Nitrogen Nutrition and Allocation by Mycorrhizal and Nonmycorrhizal *Panicum coloratum* L., a C_4 Grass

L.L. Wallace*, S.J. McNaughton, M.B. Coughenour
Syracuse University, Department of Biology, Biological Research Labs, 130 College Place, Syracuse, NY, 13210, USA

Summary. Mycorrhizal and nonmycorrhizal plants of *Panicum coloratum* L. were grown in a factorial treatment design under two nitrogen levels and two clipping heights with an unclipped control. The nitrogen concentration in different plant components was determined following 9 weeks of growth under experimental conditions. Mycorrhizal infection increased green leaf and sheath nitrogen concentration by a relatively small, but significant percentage and had no effect on nitrogen allocation to the various plant components. Clipping increased leaf nitrogen concentration but inhibited growth to the extent that, when compared with the unclipped controls, less nitrogen remained in residual plant biomass with up to half of the total nitrogen allocated to offtake (the material removed by clipping). Plants receiving the higher nitrogen fertilization had higher tissue concentration of N and more N allocated to aboveground living tissues. Mycorrhizal infection interacted with clipping height and also with N availability significantly. Infection was unable to ameliorate the negative effects of the most severe clipping regime and of the low nitrogen availability on leaf and sheath N content. This is possibly due to mycorrhizal demand for carbohydrates competing with the carbohydrate requirement of roots for nitrogen uptake.

Introduction

The effects of mycorrhizal fungi on plant growth have been well-documented (Gerdemann 1968, Harley 1969), although the mechanisms of these effects are still not clear. Mycorrhizae are known to enhance the phosphorous nutrition of their hosts and, in some cases, enhance nitrogen uptake as well (Brady 1974, Harley 1969, Ho and Trappe 1975). Both of these nutrients may be in short supply in many soils (Brady 1974).

At one point grasslands were felt to be less productive than forests, primarily because of their lower standing stock of nutrients in the vegetation and their 'leakier' nutrient cycles (Foth and Turk 1972, Odum 1971, Whittaker 1970). Current work on both tropical and temperate grasslands has shown that although the mechanisms of nutrient retention and cycling differ, climax grasslands are no more leaky than their forest counterparts (Christie 1979, Rauzi 1979, Sparrow 1979). The Serengeti grassland ecosystem of Tanzania and Kenya supports the largest community of grazing ungulates in the world (Norton-Griffiths and Sinclair, 1979) and therefore must possess effective and efficient nutrient cycling mechanisms. Nitrogen may be one of the factors limiting both plant and animal production in this tropical ecosystem (McNaughton et al. 1981).

Recent field and laboratory studies have shown that plant production in the Serengeti grassland ecosystem is enhanced by grazing (McNaughton 1976 1979; Wallace et al in preparation). Could the effects of animals on plant productivity be partially mediated by mycorrhizae and their effects on the nutrient status by a plant as well as their known contribution to nutrient conservation (Stark and Jordan 1978)? In this study we examined plant nitrogen and crude protein levels in laboratory-grown *Panicum coloratum* L., a C_4 grass common in mid-grasslands of the Serengeti, to determine whether nitrogen allocation within the plant and the nitrogen content of different plant organs were affected by mycorrhizal infection and how this interacted with grazing and fertilization regimes similar to those experienced in the field.

Materials and Methods

Twenty-four plants of *Panicum coloratum* L. were grown in an unbalanced factorial design of mycorrhizal presence, clipping height and nitrogen availability. All plants were grown in washed, sterile sand in 15 cm plastic pots, watered daily and fertilized every 4 days with modified Hoaglands, containing either 13 mM or 1 mM nitrogen as NH_4NO_3. The clipping treatments consisted of unclipped controls or clipping at 10-cm or 5-cm height every 6 days. The nitrogen and clipping treatments were based on field measurements of soil nitrogen (de Wit 1978) and grazing heights (McNaughton 1976, 1979). These values represent the range of ecologically realistic values rather than the range to which the plant could respond physiologically. Mycorrhizal plants were obtained from our laboratory stock populations and nonmycorrhizal plants were obtained by rooting cuttings in distilled water and then placing them in sterile sand in surface sterilized plastic pots. The roots of all plants were scored for mycorrhizal infection at the end of the experiment and there was very little contamination of the nonmycorrhizal plants (Wallace 1981).

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