Response of Soil Invertebrates to Clear-cutting and Partial Cutting in a Boreal Mixedwood Forest in Northern Ontario

FINAL REPORT

J.A. Addison[1] and K.N. Barber

Environmental Research and Assessment Project
Canadian Forest Service, Great Lakes Forestry Centre
Box 490
Sault Ste. Marie, ON
P6A 5M7

[1] Present Address: Applied Research Division, Royal Roads University, 2005 Sooke Road, Victoria, BC V9B 5Y2

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ABSTRACT

The short-term effects (two years) of different harvesting methods (clear-cutting and partial cutting) on soil invertebrates, including carabid beetles, Collembola (springtails), mites and fly larvae, were studied in a boreal mixedwood forest in northern Ontario.

A significant reduction in the abundance of mites (one year post-harvest) and fly larvae (two years post-harvest) was found in the clear-cuts compared with the uncut forest. Overall abundance of Collembola, or the capture rate of carabids were not affected by the different harvesting regimes. However, in these groups, treatment-related effects were detectable at the species level. Changes in species richness and species diversity, as well as in the relative contribution of individual species to their respective communities, were all affected by harvesting. For carabids, these changes involved the addition of species with a preference for clear-cut conditions, as well as a re-structuring of the community already resident on the sites. For Collembola, there was no evidence of immigration of new species adapted to clear-cut conditions in the first two years post-harvest. Changes in the community in response to harvesting were caused by changes in the relative proportions of species already present on the sites.

The extremely hot and dry weather conditions experienced in the summer of 1995 had a profound effect on the abundance of Collembola in all treatment areas including the uncut forest, whereas reductions in numbers of fly larvae occurred only on partial cuts and the clear-cuts. Numbers of carabids and mites were not affected by the drought.

Preliminary studies into the biological impacts of logging trails indicated harvesting by the Timberjack caused little or no damage to microarthropod populations. Reductions in mite and collembolan population levels were evident on trails made by the feller-buncher or single-grip harvester, but there was evidence of some recovery in population numbers by the second year post-harvest.

The report concludes with a discussion of effects of natural and man-made disturbance on soil invertebrates, and recommendations for minimizing harvesting impacts on the community.

RÉSUMÉ

Les effets à court terme (2 ans) de 2 méthodes de récolte (coupe à blanc et coupe partielle) sur les invertébrés terricoles, y compris les carabes, les collemboles, les acariens et les larves de mouches, ont été étudiés dans une forêt mixte boréale du nord de l'Ontario.

Une forte baisse du nombre d'acariens (1 an après la récolte) et de larves de mouches (2 ans après la récolte) a été constatée dans les coupes à blanc par rapport à la forêt non abattue. L'abondance globale de collemboles ou le taux de capture de carabes n'ont pas été affectés par les différents modes de récolte. Cependant, dans ces groupes, des effets liés au traitement étaient décelables au niveau de l'espèce. La récolte a modifié la richesse et la diversité spécifiques ainsi que la contribution relative des espèces individuelles à leurs communautés respectives. Pour les carabes, ces changements ont entraîné l'addition d'espèces, notamment dans le régime de coupe à blanc, de même qu'une restructuration de la communauté vivant déjà sur les sites. Pour les collemboles, aucune immigration de nouvelles espèces adaptées à la coupe à blanc n'a été constatée dans les 2 premières années suivant la récolte. Des changements dans la communauté en réaction à la récolte ont été provoqués par des modifications dans la composition des espèces déjà présentes sur les sites.)

Les conditions météorologiques extrêmement chaudes et sèches qui ont sévi à l'été 1995 ont eu un effet profond sur l'abondance des collemboles dans toutes les zones traitées, y compris la forêt non abattue, tandis que les réductions du nombre de larves de mouches se sont limitées aux coupes partielles et aux coupes à blanc. Les effectifs de carabides et d'acariens n'ont pas été touchés par la sécheresse. Des études préliminaires sur les impacts biologiques des chemins de débusquage ont indiqué que la récolte effectuée par le Timberjack a causé peu ou point de dommages aux populations de microarthropodes. Les populations d'acariens et de collemboles ont chuté sur les chemins faits par l'abatteuse-empileuse ou l'abatteuse-façonneuse à tête multifonctionnelle, mais elles ont semblé se rétablir quelque peu dès la deuxième année après la récolte.

Le rapport se termine par une étude des effets des perturbations naturelles et anthropiques sur les invertébrés terricoles ainsi que par des recommandations visant à atténuer au maximum les incidences de la récolte sur la communauté.

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INTRODUCTION

Forest managers today are required not only to ensure a sustainable wood supply, but are under increasing pressure to manage forests as ecosystems, preserving and promoting a wide array of non-timber values including biological diversity, old-growth forests, wildlife habitat, recreational opportunities, and spiritual values (Canadian Council of Forest Ministers 1992, Ontario Ministry of Natural Resources 1995). Since Ontario boreal mixedwoods typically occupy fertile sites, these forests are potentially very productive, both in terms of the richness of flora and fauna, and in terms of timber yield. Management of these forests has typically involved clear-cutting, followed by silvicultural interventions to establish a conifer-rich stand. There is growing national and international concern over conventional timber management practices, particularly clear-cutting and the extensive planting of single species stands (Brooks and Grant 1992, Mooney et al. 1995); research into the suitability and environmental consequences of alternative management options is urgently required.

Biodiversity is one parameter by which the "health" of an ecosystem can be assessed, yet many of the organisms responsible for ecosystem health and sustainability (e.g., microorganisms and invertebrates) reside in the soil, and their importance is often overlooked (Freckman1994). Many soil invertebrates are known to play important roles in nutrient cycling, pest control, dispersal of mycorrhizal fungi, controlling (or dispersing) plant pathogens, soil formation and decomposition of plant residues including leaf litter, roots, and woody materials, all representing an integral part of sustainable forestry (Marshall 1993). Not only do researchers and managers not know how "alternative" forestry practices affect these organisms and their processes, they know very little about how they respond to conventional practices (such as clear-cutting), or natural disturbances such as fire or drought. Indeed the Canadian Biodiversity Strategy (Government of Canada 1995) recommends the inventory and monitoring of the forest soil biota to help increase our understanding of forest biodiversity.

This study reports on the short-term impacts of conventional (clear-cutting) and alternative (partial cutting) harvesting practices on the abundance and biodiversity of elements of the soil fauna. This study is part of the Black Sturgeon Boreal Mixedwood Project, a multidisciplinary research project focusing on stand-level ecosystem response to disturbance and silvicultural manipulation (Scarratt 1996). Two groups of soil fauna were included in the study:

1. Ground-dwelling carabid beetles
2. Soil-dwelling microarthropods (Collembola [springtails], Acari [mites] and Diptera [fly] larvae).

It has been estimated that only about 50 percent of the arthropod species in Canadian soils have been described (Behan-Pelletier and Bissett 1992). In comparison with other groups of soil fauna, the taxonomy of carabids and Collembola is relatively well known, and keys to species are available. Thus it was possible to investigate the response of these groups to harvesting at the species level.

Carabid beetles have been widely used as bioindicators of ecological disturbance in Canada and around the globe. Carabids have been used to investigate non-target effects of forestry insecticides (Freitag et al. 1969, Freitag and Poulter 1970). The various studies by Richardson and Holliday (Richardson and Holliday 1982; Holliday 1984, 1991, 1992) documented the response of carabid beetles to wild fire in stands of trembling aspen (*Populus tremuloides* Michx.) and spruce (*Picea* spp.). Niemelä et al. (1993a, 1993b) discussed the effects of clear-cut harvesting on assemblages of carabids in boreal forests by comparing stands at various stages of regeneration. The immediate response of carabids to planned clear-cutting and to prescribed burning in stands of jack pine (*Pinus banksiana* Lamb.) was described by Duchesne and McAlpine (1993).

In Europe, soil microarthropods (Collembola and mites) have been used as indicators of acid precipitation (e.g., van Straalen et al. 1988), soil compaction (e.g., Heisler 1995) and agricultural practices (e.g., Franchini and Rockett 1996). The use of soil invertebrates as "biological probes" of complex soil phenomena in old-growth forests of the Pacific Northwest was proposed by Moldenke and Lattin (1990a). Before attempts can be made to identify "bioindicators" of forest soil health in Canada, more knowledge of the identity and classification of soil arthropods, their distribution, feeding habits and response to environmental stress is required.

SITE DESCRIPTION AND EXPERIMENTAL TREATMENTS

The site is located in the Black Sturgeon Forest, approximately 120 km northeast of Thunder Bay, Ontario. The stands can be classified as herb- and shrub-rich vegetation types according to the forest ecosystem classification for northeastern Ontario (V6, V7, V9, V11, V16; Sims et al. 1989), with the dominant tree species being trembling aspen, balsam fir (*Abies balsamea* [L.] Mill.), white spruce (*Picea glauca* [Moench] Voss), and black spruce (*Picea mariana* [Mill.] B.S.P.). The soils are Ferro-humic Podzols and Dystric Brunisols. Each experimental block consisted of an area of 10 ha, with 100 m wide uncut buffer zones between the blocks. Two replicates of each harvesting treatment were located in Stand 1 (49° 11' 15" N and 88° 42' 30" W), with a third replicate in Stand 2 (49° 14' 03" N and 88° 45' 30" W). Each clear-cut block was divided to permit one half to be site prepared (clear-cut B), while the other half remained untreated (clear-cut A). Details of the site description and harvesting treatments are given in Scarratt (1996). Harvesting took place in the fall and winter of 1993, and site preparation treatments were applied in August 1995. The Fire Ecology component of the study (Burn Blocks) contained additional replicates of the clear-cut treatment and uncut controls, and these were included in the microarthropod study. Because of unfavourable weather conditions, it was not possible to carry out the prescribed burn treatments during the period covered by this report. A summary of the experimental harvesting treatments included in the present study is given in Table 1.

MATERIALS AND METHODS

Carabids

Carabid beetles were sampled with twelve 1 L plastic pitfall traps, (11 cm diameter), protected from rain with plastic dinner plates elevated slightly above the soil surface. Two parallel lines 40 m apart, with six traps each, were installed on each block. The traps were spaced 10 m apart. On clear-cuts, two pitfall lines were run on each of side A and side B. Ethylene glycol was used as a collection and preservative fluid. Traps were emptied about every two weeks and their contents transferred to 70 percent ethanol. Carabid beetles were then extracted, pinned, labeled, and identified according to Lindroth (1961–1969) and Bousquet and Larochelle (1993).

Seven samples were taken in each of 1994 and 1995 (early June to early September) but only the four odd-numbered samples were processed. The clear-cut B treatment is not included in the various ANOVA procedures because sample number five is missing as traps were removed to allow for the site preparation treatment. The cumulative catch for this treatment thus represents both pre- and post-site preparation conditions. However, the capture data for clear-cut B is included in histograms and other discussions. Because preparations for the prescribed burns required the removal of pitfall traps from the Burn Blocks, data for these sites were incomplete and are not included in this report.

Microarthropods

Two 10 x 10 m plots were established in each of the experimental blocks presented in Table 1, with the exception of Stand 1, Blocks 5 and 7. On all treatment blocks in

Table 1. Summary of blocks and harvesting treatments included in the present study.

Treatment	Harvesting equipment	Blocks	Studies[1]
Clear-cut Full-tree extraction	Feller-buncher, grapple skidder	Stand 1, Blocks 1 and 14 Stand 2, Block 6 Burn Blocks 1 and 5	C, M, T C, M M
Clear-cut Tree-length extraction	Single-grip harvester (Ultimate 4500), grapple skidder	Stand 1, Block 7	T
Partial Cut - 70 percent removal Full-tree extraction	Feller-buncher, grapple skidder	Stand 1, Blocks 2 and 3 Stand 2, Block 4	C, M, T C, M
Partial Cut - 70 percent removal Cut-to-length	Single-grip harvester (Timberjack 1270) and forwarder (Timberjack 1010)	Stand 1, Block 5	T
Uncut controls		Stand 1, Blocks 4 and 13 Stand 2, Block 5 Burn Blocks 3,6 Sanders/Prévost	C, M C, M M M

[1]C included in study of carabids
M included in study of microarthropods
T included in study of microarthropod fauna in transects across logging trails

Stands 1 and 2, one plot was located on side A and the other on side B, close to the pitfall traps where applicable. On the Burn blocks and the Sanders/Prévost control block, which were not divided into side A and side B, samples were taken from plots located near the pitfall traps. Each core (5.8 cm diameter) was taken to a minimum depth of 10 cm, and included the entire organic layer, and at least 2 cm of the underlying mineral soil. Cores were divided into 2-cm sections, the sample was weighed, and the fauna were extracted into distilled water in a modified Macfadyen High Gradient extractor over a period of a week. After extraction of the fauna, the samples were re-weighed and moisture content was estimated.

The extracted fauna were filtered from the collecting fluid using a Millipore Filtration unit, and stored in 70 percent ethanol. Mites and dipteran larvae were counted under a dissection microscope. Preliminary sorting of Collembola into morphological groups was carried out using the dissection microscope, but final species identification required most individuals to be cleared in lactic acid, mounted in Hoyer's medium and examined under high magnification using oil-immersion and phase contrast lighting. The taxonomic keys of Christiansen and Bellinger (1980a, 1980b, 1980c, 1981) were used to identify Collembola to species.

Plots were sampled three times in 1994 (spring, summer, fall), and twice in 1995 (spring, summer). At each time of sampling, one core was taken from each plot, and the data from the two cores/block were pooled to give a single value for each replicate block.

A preliminary study of the impacts of the logging trails created by different types of harvesting machinery was carried out on selected blocks in Stand 1 as indicated in Table 1. On each block, the main logging trail was subjectively identified. In early June 1994, a transect was run across the trail, approximately 50 m from the edge of the cut block nearest the road, perpendicular to the line of travel. A core of soil was taken 50 cm from each edge of the logging trail in the relatively undisturbed soil on each side of the trail, and two cores were taken on the trail, each one 2 m from the edge of the trail. The same transect was sampled again in late May 1995. Microarthropods were extracted and processed as described above.

Statistical Analyses

Histograms of the abundance of individual species of carabids for 1994 and 1995 are expressed as proportions of the total cumulative catch taken from each replicate block. Preliminary statistical analyses are based on separate treatment of the data sets of 1994 and 1995, representing cumulative catches (sum of four samples) of each replicate block. Carabid catches were also standardized by the number of trapnights to compensate for some losses of traps disturbed by mammals. Analysis of variance (ANOVA) tests were carried out using BMDP (BMDP Statistical Software Inc.) and SigmaStat (Jandel Scientific) software. In the one-way ANOVA tests, experiment-wise error rate was maintained at α=0.05 using a sequential Bonferroni adjustment (Rice 1989). Transformations were applied if necessary; proportional data and evenness indices were arcsine-transformed. Only the non-transformed means and standard errors are reported. We used the discussions, recommendations, and software of Ludwig and Reynolds (1988) to direct, compute and present diversity indices. "N0" represents species richness (number of species) while the species diversity indices "N1" (number of abundant species) and "N2" (number of very abundant species) (Hill 1973) incorporate both species richness and species equitability (relative abundance of different species).

RESULTS

Effect of Harvesting on Total Numbers of Individuals Collected

Carabids

A total of 1 415 and 2 214 carabid beetles were captured over four treatments in 1994 and 1995, respectively. Seasonal capture rates of carabids standardized to 100 trapnights did not differ among treatments in either 1994 or 1995 (Table 2).

Microarthropods

In the first year post-harvest, numbers of dipteran larvae in cores taken from the different harvesting treatments did not differ significantly among treatments. However, in 1995 there was a significant reduction in the abundance of larvae on the clear-cuts compared with controls, while on partial cuts the value was intermediate between the two extremes (Table 3).

The overall seasonal abundance of mites was reduced on the clear-cuts in the first year post-harvest, compared with the uncut controls (Table 4). In the second year post-harvest, mites were significantly less abundant in the clear-cuts than in the partial cuts, but the numbers of mites in the uncut controls did not differ significantly from levels found in the clear-cuts.

Harvesting did not significantly affect the overall seasonal abundance of Collembola in either 1994 or 1995 (Table 5).

Table 2. Effect of harvesting on capture rate of carabids. Means are calculated from seasonal totals for each replicate block. ANOVA revealed no significant treatment effects in either year (1994 P=0.1744; 1995 P=0.2688).

Treatment	Number of replicates	Mean number of individuals ± SE /100 trapnights	
		1994	1995
Uncut controls	3	22.0 ± 2.9	30.9 ± 4.7
Partial cuts	3	13.8 ± 0.8	27.0 ± 3.9
Clear-cut A	3	16.6 ± 2.1	23.6 ± 3.3
Clear-cut B	3	22.1 ± 4.3	NA

Table 3. Effect of harvesting on abundance of dipteran larvae. Means are calculated from seasonal totals for each replicate block. ANOVA of 1994 data for treatment effects, P=0.520; for 1995 P=0.003. Within each time period, means not followed by the same letter differ significantly from one another (sequential Bonferroni t-tests; P<0.05).

Treatment	Number of replicates	Mean number of individuals ± SE /m^2	
		1994	1995
Uncut controls	6	2 142 ± 858	1 181 ± 77 a
Partial cuts	3	1 070 ± 787	503 ± 269 ab
Clear-cut	5	1 033 ± 466	189 ± 79 b

Table 4. Effect of harvesting on abundance of mites. Means are calculated from seasonal totals for each replicate block. ANOVA for treatment effects for 1994 P=0.016; for 1995 P=0.019. Within each time period, means not followed by the same letter differ significantly from one another (sequential Bonferroni t-tests; P<0.05).

Treatment	Number of replicates	Mean number of individuals ± SE /m^2	
		1994	1995
Uncut controls	6	179 517 ± 9 384 a	189 710 ± 18 451 ab
Partial cuts	3	134 976 ± 9 619 b	228 793 ± 23 974 a
Clear-cut	5	129 686 ± 14 004 b	130 379 ± 16 098 b

Table 5. Effect of harvesting on abundance of Collembola. Means are calculated from seasonal totals for each replicate block. ANOVA revealed no significant treatment effects in either year (1994 P=0.929; 1995 P=0.246).

Treatment	Number of replicates	Mean number of individuals ± SE /m^2	
		1994	1995
Uncut controls	6	53 285 ± 9 514	36 720 ± 4 030
Partial cuts	3	51 773 ± 7 059	47 616 ± 4 101
Clear-cut	5	49 242 ± 3 959	47 333 ± 6 191

Effect of Harvesting on Species Diversity

Carabids

In both the first and second years post-harvest, the mean number of species captured/ replicate block (N0) was significantly lower in at least one of the clear-cuts (A or B) than in the uncut controls (Tables 6 and 7). The number of abundant species (N1) was apparently unaffected by the treatments in both years, but values for N2 (number of very abundant species) showed clear treatment-related effects. In both 1994 and 1995, values for N2 were significantly lower in the clear-cuts than in the uncut controls, while values on the partial cut were intermediate between the two extremes (although differing significantly from the clear-cuts and uncut controls only in 1994). The Evenness Index (E5) was highest in the uncut controls in both years, decreasing on the partial cuts, and was lowest in the clear-cuts.

Collembola

In the first year post-harvest, the number of abundant species (N1) was significantly depressed on the clear-cuts compared with the uncut and partial cuts, and N2 was reduced on the clear-cuts compared with partial cuts (Table 8). Values for N0 and the Evenness Index showed no significant treatment-related differences. In the second year post-harvest, values for the diversity and evenness indices did not differ significantly among treatments (Table 9).

Table 6. Effect of harvesting on species diversity indices and evenness of carabids one year post-harvest. Indices calculated after Hill (1973) using seasonal totals for each replicate treatment block. N0 is the total number of species, N1 is $e^{\text{Shannon's Index}}$, N2 is 1/Simpson's Index, and Evenness Index is (N2-1)/(N1-1). ANOVA revealed significant treatment effects on N0 (P=0.0237), N2 (P<0.001) and the Evenness Index (P<0.001). There was no significant treatment effect on N1 (P=0.0528). Within each column, means not followed by the same letter differ significantly from one another (sequential Bonferroni t-tests, P<0.05).

	N0	N1	N2	Evenness Index
Uncut controls	8.7 a	6.2	5.6 a	0.89 a
Partial cut	9.7 ab	5.5	4.2 b	0.70 b
Clear-cut A	10.7ab	4.7	3.0 c	0.55 c
Clear-cut B	12.7 b	4.5	2.6 c	0.46 d

[1] Shannon's Index = $$\hat{H}' = -\sum_{i=1}^{S}\left[\left(\frac{n_i}{n}\right)\ln\left(\frac{n_i}{n}\right)\right]$$

[2] Simpson's Index = $$\hat{\lambda} = \sum_{i=1}^{S}\frac{n_i(n_i-1)}{n(n-1)}$$

where n_i is the number of individuals in the i^{th} species and n is the total number of individuals for all species in the sample.

Table 7. Effect of harvesting on species diversity indices and evenness of carabids two years post-harvest. Indices as in Table 6. ANOVA revealed significant treatment effects on N0 (P=0.014), N2 (P=0.035) and the Evenness Index (P=0.003). There was no significant effect of treatment on N1 (P=0.141). Within each column, means not followed by the same letter differ significantly from one another (sequential Bonferroni t-tests, P<0.05).

	N0	N1	N2	Evenness Index
Uncut controls	10.0 a	6.6	5.7 a	0.83 a
Partial cut	13.7 ab	7.0	5.1 ab	0.67 b
Clear-cut A	16.3 b	5.5	3.2 b	0.49 c

Table 8. Effect of harvesting on species diversity indices and evenness of Collembola one year post-harvest. Indices calculated as in Table 6. ANOVA revealed no significant treatment effects on N0 (P=0.232) or the Evenness Index (P=0.568). Treatment related effects were identified for N1 (P=0.008) and N2 (P=0.0260). Within each column, means not followed by the same letter differ significantly from one another (sequential Bonferroni t-tests, P<0.05).

	N0	N1	N2	Evenness Index
Uncut controls	25.8	9.6 a	6.2 ab	0.595
Partial cut	24.0	9.9 a	7.0 a	0.673
Clear-cut	20.6	6.9 b	4.5 b	0.600

Table 9. Effect of harvesting on species diversity indices and evenness of Collembola two years post-harvest. Indices as in Table 6. ANOVA detected no significant treatment effects on N0 (P=0.452), N1 (P=0.199), N2 (P=0.375) or the Evenness Index (P=0.950).

	N0	N1	N2	Evenness Index
Uncut controls	20.3	9.5	7.3	0.671
Partial cut	20.0	10.2	7.4	0.695
Clear-cut	18.2	6.9	5.0	0.665

Effect of Harvesting on Individual Species

Carabids

A total of 34 species of carabids was collected over the two years; 23 species in 1994 and 31 species in 1995 (Figs. 1 and 2). Five species (*Pterostichus adstrictus* Eschscholtz, *Pterostichus pensylvanicus* LeConte, *Calathus ingratus* Dejean, *Platynus decentis* (Say), and *Sphaeroderus nitidicollis brevoorti* LeConte) were captured on all 12 blocks in both years, collectively comprising 81–90 percent and 81–84 percent of captures in 1994 and 1995 respectively. In the first year post-harvest, there was a significant increase in the proportional representation of *P. adstrictus* in the carabid community from uncut to partial cut to clear-cut treatments. There was a corresponding trend toward a decreasing contribution of the other four species (not always statistically significant) in the same sequence. In 1995, only *P. adstrictus* and *P. decentis* showed significant treatment differences in proportional representation similar to those observed in 1994, but in *S. nitidicollis* and *P. pensylvanicus* the trend toward decreasing abundance on the clear-cuts was still present (although not statistically significant). In addition to these five species, *Agonum retractum* LeConte was captured on all blocks except one clear-cut A block and represented another 3–8 percent of captured carabids, but there were no significant treatment differences in either year for this species (Table 10).

Three species (*Bembidion rapidum* LeConte, *Notiophilus semistatus* Say, *Badister obtusus* LeConte), represented by only one or two specimens in 1994, were not recovered in 1995. Of the eleven species collected in 1995 that had not been captured in 1994, eight (*Bradycellus lugubris* LeConte, *Sericoda quadripunctatua* (DeGeer), *Harpalus laevipes* Zetterstedt, *Harpalus somnulentus* Dejean, *Bembidion mutatum* Gemminger and Harold, *Bembidion grapii* Gyllenhal, *Bembidion wingatei* Bland, *Bembidion quadrimaculata oppositum* Say) were represented by three or fewer specimens. Only five specimens of *Agonum cupripenne* Say were taken in 1995, all in the clear-cut B treatment. These captures were made prior to the site preparation treatment so are not related to this disturbance. *Harpalus innocuus* LeConte, represented by 19 specimens, was taken only on the six clear-cut blocks, while 47 specimens of *Calosoma frigidum* Kirby were taken from all treatments.

Of those species for which more than three specimens were collected in one year, species present in uncut forest were also found in at least one block of the other three treatments except in two instances. Although *Pterostichus coracinus* (Newman) (four specimens) was not collected in the uncut forest in 1994, the next year, five specimens were taken from the uncut and the partial cut forest. *Scaphinotus bilobus* (Say) (39 specimens) occurred on all blocks except one uncut block in 1994. However, in 1995, 38 specimens were captured but none were taken from one partial cut block nor from any of the three blocks of the clear-cut B treatment.

Calosoma frigidum was first captured in 1995 (47 specimens), two years after the harvest. This species formed a significantly higher proportion of the carabid fauna in the

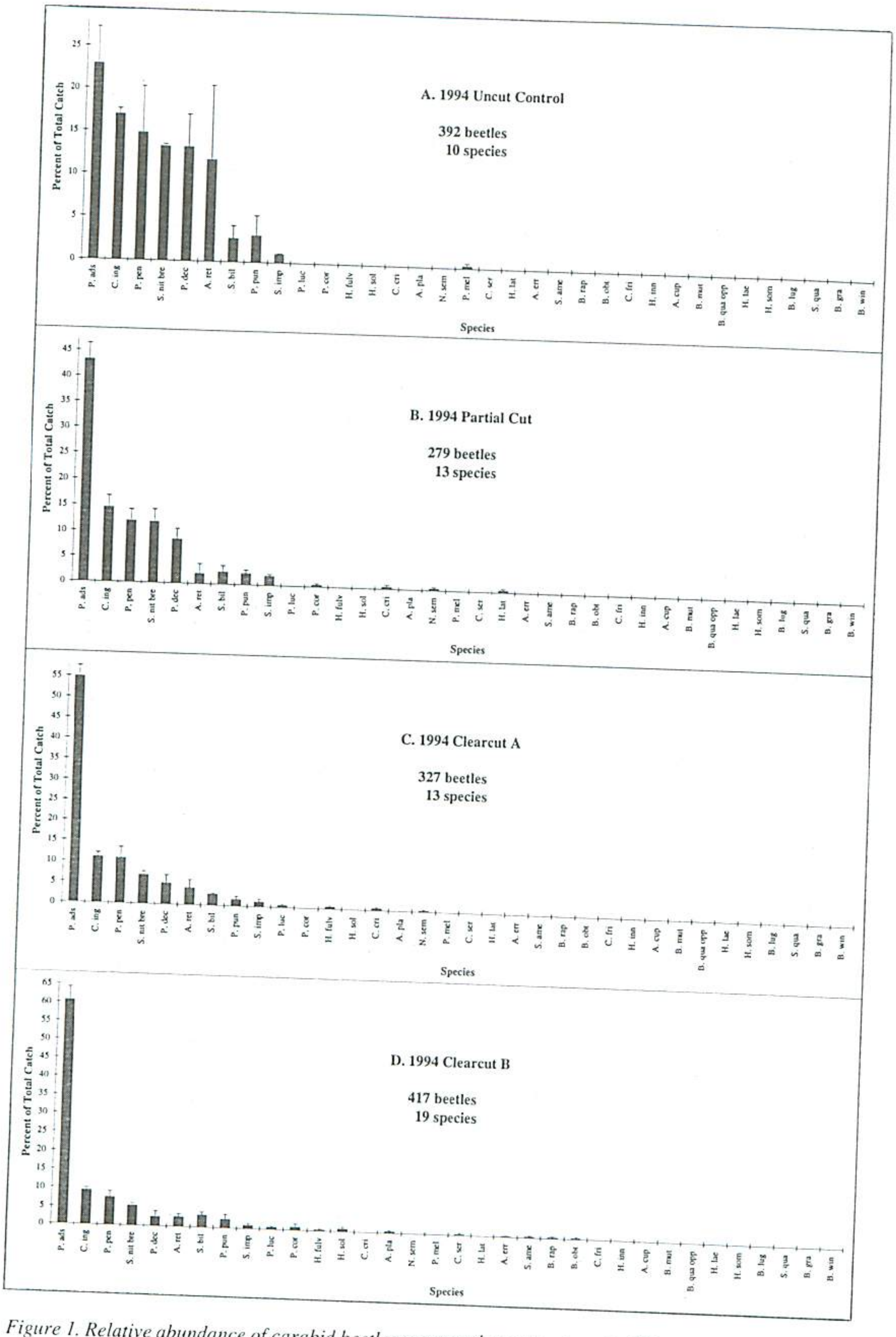

Figure 1. Relative abundance of carabid beetles expressed as percentage (+ SE) of total seasonal catch (four collections) in each treatment block (n=3) for 1994, one year after harvest. A. uncut control; B. partial cut; C. clear-cut A; D. clear-cut B. See Appendix A for species names.

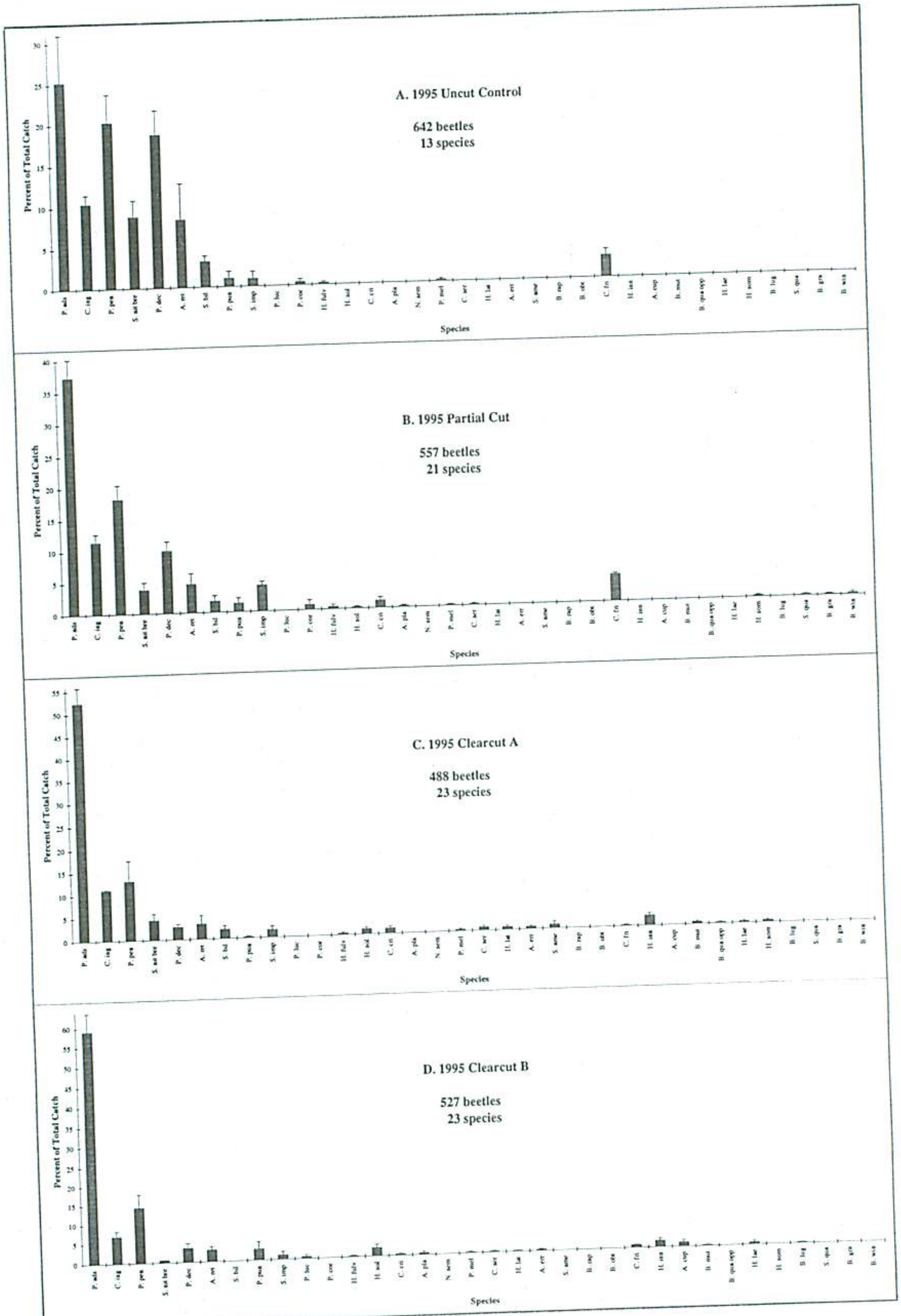

Figure 2. Relative abundance of carabid beetles expressed as percentage (+ SE) of total seasonal catch (four collections except clearcut B with three) in each treatment block (n=3) for 1995, two years after harvest. A. uncut control; B. partial cut; C. clear-cut A; D. clear-cut B. See Appendix A for species names.

Table 10. Relative abundance of selected carabid species based on cumulative seasonal samples. Data based on four sampling periods each year. Figures are mean percentage of total carabids/replicate block. There were three uncut replicates, three partial cut and three clear-cut A and three clear-cut B replicates. Data from clear-cut B in 1995 not included in analyses as site preparation treatments were imposed on these replicates part way through the year. One-way ANOVA was performed within each time period to detect treatment effects. Within each row, means not followed by the same letter differ significantly from one another (sequential Bonferroni t-tests, P<0.05).

Species	Year	Treatment				
		Uncut	Partial cut	Clear-cut A	Clear-cut B	ANOVA
Pterostichus adstrictus	1994	22.9 a	43.2 b	54.9 bc	60.7 c	P<0.001
	1995	25.2 a	37.3 ab	52.4 b	NA	P=0.010
Pterostichus pensylvanicus	1994	14.8	12.0	10.8	7.7	P=0.533
	1995	20.2	18.1	13.1	NA	P=0.398
Calathus ingratus	1994	17.0 a	14.5 ab	11.0 ab	9.4 b	P=0.016
	1995	10.4	11.4	11.1	NA	P=0.758
Platynus decentis	1994	13.2	8.6	5.0	2.6	P=0.081
	1995	18.6 a	9.9 b	2.8 c	NA	P=0.004
Sphaeroderus nitidicollis	1994	13.3 a	11.9 ab	6.9 ab	5.6b	P=0.010
	1995	8.7	3.8	4.3	NA	P=0.121
Agonum retractum	1994	11.8	1.9	4.0	2.7	P=0.457
	1995	8.3	4.5	3.4	NA	P=0.489
Calosoma frigidum	1994	0.0	0.0	0.0	0.0	
	1995	2.7 a	4.2 a	0.2 b	NA	P=0.003
Harpalus spp.	1994	0.0	0.4	0.6	1.1	P=0.492
	1995	0.2 a	0.7 a	4.9 b	NA	P=0.004

uncut and partial cut forest than in the clear-cuts. Several species of *Harpalus* were captured through 1994 and 1995, with more specimens and species in 1995 (Table 11). Although there was a trend towards larger numbers of individuals and species, from control through partial cut and then the clear-cuts in both years, only the 1995 data show a significantly higher value for the proportional representation of *Harpalus* spp. on clear-cuts compared with uncut forests (Table 10).

Table 11. Captures of *Harpalus* spp. for mixedwood forest blocks in 1994 and 1995, based on cumulative seasonal samples[1].

Year	Parameter	Treatment				Total
		Uncut	Partial cut	Clear-cut A	Clear-cut B[2]	
1994	Individuals	0	1	2	4	7
	Species	0	1	1	2	2
1995	Individuals	1	4	23	23	51
	Species	1	3	6	5	6

[1] Cumulative seasonal totals based on two week trapping periods carried out four times in 1994 (June, July, August, September), and four times in 1995 (June, July, August, September; except Clear-cut B where August was missed to allow site preparation treatment)

[2] Site preparation treatment applied in August 1995

Collembola

More than 17 500 Collembola, representing 42 species were collected over two years. *Folsomia nivalis* (Packard) was the most widespread and abundant species, and was common in all blocks, regardless of harvesting regime. When present in a sample, *Ceratophysella* sp. (probably *pseudarmata*) (Folsom) showed an extremely aggregated distribution, but since this species occurred in relatively few samples (even in the uncut controls where it formed 13.1 percent of the total collembolan population), it was not possible to use parametric statistics to describe the population of this species. Some species such as *Isotomiella minor* (Schäffer), and *Onychiurus (Protaphorura) parvicornis* Mills tended to be relatively more abundant in the clear-cuts than in the uncut areas. Other species, including *Folsomia sensibilis* Kseneman, *Isotoma (Desoria) propinqua* Axelson and *Arrhopalites benitus* (Folsom) were relatively more abundant in uncut forests (although this preference was only statistically significant in one of the two years). In species showing a preference for clear-cuts over uncut blocks, or vice versa, values for the partial cuts were generally intermediate between the 2 extremes (Table 12).

Only three species of Collembola were collected on the clear-cuts or partial cuts, but not in the uncut forest, and in all three cases fewer than 5 individuals of each species were collected. *Folsomia* sp. A (33 individuals), *Proisotoma (Appendisotoma) vesiculata* Folsom (11 individuals) and *Isotoma (Desoria)* sp. A (20 individuals) and another 4 species with fewer than 5 individuals/species, were all collected in uncut or partial cuts, but not in samples taken from clear-cuts.

Effect of Drought—Comparison of August 1994 and 1995 Samples

During the summer of 1995, weather conditions were very dry, and forest fires were burning in areas within a few kilometers of the research sites. A full set of micrometeorological data for the sites is not yet available, but preliminary data (Boyonoski pers. comm.) indicate that in August 1995, soil temperatures just below the soil surface (-1 cm) were about 2–4°C higher in the clear-cuts (mean maximum weekly temperature 23°C) than in the uncut sites (mean maximum weekly temperature 19°C). Temperatures were intermediate between the two extremes in the partial cut (mean maximum weekly temperature 21°C).

Table 12. Relative abundance of species of Collembola based on cumulative seasonal samples. There were three sampling periods in 1994, and two in 1995. Figures are mean percentage of total Collembola /block. There were six uncut replicates, three partial cut and five clear-cut blocks. One-way ANOVA was performed within each time period to detect treatment effects. Within each row, means not followed by the same letter differ significantly from one another (sequential Bonferroni t-tests, $P<0.05$). ANOVA on ranks (KW) followed by Dunn's test was carried out where assumptions for ANOVA could not be met.

Species	Year	Treatment			ANOVA
		Uncut	Partial cut	Clear-cut	
Folsomia nivalis	1994	29.2	27.8	40.2	P=0.067
	1995	32.5	13.4	28.4	P=0.095
Onychiurus (Protaphorura) absoloni	1994	8.1	7.1	5.4	P=0.446
	1995	5.8	3.4	5.6	P=0.333
Onychiurus (Protaphorura) parvicornis	1994	0.8	5.1	3.6	P=0.200
	1995	0.2a	1.3ab	4.4b	P=0.033
Isotomiella minor	1994	0.8a	5.5b	0.7a	P=0.001
	1995	4.0a	25.9b	25.0b	$P=0.025^{kw}$
Ceratophysella sp. (probably *pseudarmata*)	1994	13.1	0.3	0.6	$P=0.175^{kw}$
	1995	0.1	0.0	0.1	$P=0.861^{kw}$
Folsomia sensibilis	1994	2.8a	1.4ab	0.7b	P=0.040
	1995	3.2	2.7	1.0	$P=0.110^{kw}$
Isotoma propinqua	1994	1.3a	1.2ab	0.2b	P=0.035
	1995	0.6	1.3	0.0	P=0.270
Arrhopalites benitus	1994	1.5	2.6	0.8	P=0.224
	1995	6.8a	3.7ab	0.6b	P=0.009

Moisture content data obtained from the cores used in the microarthropod study (Fig. 3) indicate that in all treatments, water content of the soil and organic matter in 1995 was about 50 percent of the levels measured during the previous summer. Significant reductions in the moisture content of the 0–2 cm, 2–4 cm and 4–6 cm depths on all treatments were noted in 1995 compared with 1994, but these reductions in moisture content did not depend on the type of harvesting (2-way ANOVA: 0–2 cm, treatment $P=0.534$, time $P<0.001$, treatment x time $P=0.924$; 2–4 cm, treatment $P=0.416$, time $P<0.001$, treatment x time $P=0.956$; 4–6 cm, treatment $P=0.067$, time $P<0.001$, treatment x time $P=0.083$). A detailed comparison of the August 1994 and August 1995 samples was carried out to investigate the response of the different faunal groups to the extreme environmental conditions prevailing in the summer of 1995.

Carabids

The capture rate of carabids (no./100 trapnights) did not differ significantly between August 1994 and August 1995 (Table 13).

Microarthropods

Data for the dipteran larvae (Table 14) show that in addition to an overall reduction in number of individuals sampled in August 1995 compared with August 1994, this reduction depended on the type of harvesting treatment. Values for dipteran larvae in the uncut controls did not differ significantly from one another in the two summers, but in the clear-cuts and partial cuts, the abundance of fly larvae was significantly reduced in August 1995 compared with August 1994.

A comparison of mite numbers in the two sets of summer samples indicated no significant time or treatment effects (Table 15), although there was a significant interaction term. This was due to a significant increase in the numbers of mites in the partial cuts in 1995 compared with levels at that time in the previous year.

The abundance of Collembola in August 1995, during a period of drought, was significantly reduced, compared with levels sampled the previous year. However, this reduction in population numbers occurred in all treatments, including the uncut controls, and there was no evidence that the numbers of Collembola were reduced less (or more) in the uncut blocks than in blocks that had been harvested (Table 16).

The major reduction in collembolan numbers in the dry, hot summer of 1995 occurred in the uppermost layers of the soil in all treatments, particularly the 0–2 cm depth (2-way ANOVA, treatment $P=0.255$, time $P<0.001$, treatment x time $P=0.402$) (Fig. 4). There was no increase in numbers of Collembola being collected at the lower depths, giving no evidence that individuals moved down the soil profile to avoid unfavourable conditions in the top few centimeters of soil. This drastic reduction in the numbers of Collembola extracted from the top 0–2 cm layer of soil was as apparent in the samples taken from the uncut forest as it was in those obtained from the partial cuts and clear-cuts. There was no detectable effect of either treatment or time on collembolan numbers (2-way ANOVA: treatment $P=0.725$, time $P=0.467$, treatment x time $P=0.060$) lower in the soil profile (4–6 cm)

Impacts of Logging Trails on Soil Collembola and Mites

Results obtained for Collembola and mites were very similar, and data are thus presented for one group or the other, but not for both.

In the first year post-harvest, a clear reduction in the numbers of both Collembola and mites was seen in cores taken from the logging trails of all blocks, with the possible exception of Stand 1 Block 5, which had been harvested with the Timberjack (Fig. 5, showing representative mite data; Collembola data are similar). By the second year post-harvest, there was generally some evidence of recovery in the numbers of microarthropods on the trails, but in all blocks except the one harvested by the Timberjack, the effect of the disturbance on the trails could still be seen (Fig. 5).

Results obtained in the second year post-harvest on the clear-cut logging trails suggested that the environmental impacts of trails made by the feller-buncher and grapple skidder were similar to the impacts of the single-grip harvester and grapple skidder (data for Collembola are shown in Fig. 6). Two years post-harvest, the impacts of the trails on microarthropod numbers were still visible. On the partial cuts, the effect of the trails made by the feller-buncher and grapple skidder (Stand 1 Blocks 2 and 3) on microarthropod numbers was still apparent (Fig. 7). However, there was no evidence that microarthropod numbers had been adversely affected on the trail made by the Timberjack (Stand 1 Block 5). The 2 cores taken from the logging trail actually contained more individuals than the cores taken from the undisturbed soil beside the trail.

To investigate whether the presence of decomposing woody material in cores taken from clear-cut logging trails had any effect on microarthropod numbers, the data from pairs of cores taken from the same transect at the same time, where one member of the pair contained wood and the other did not, were compared (paired t-tests on log transformation of original counts). Data from single-grip

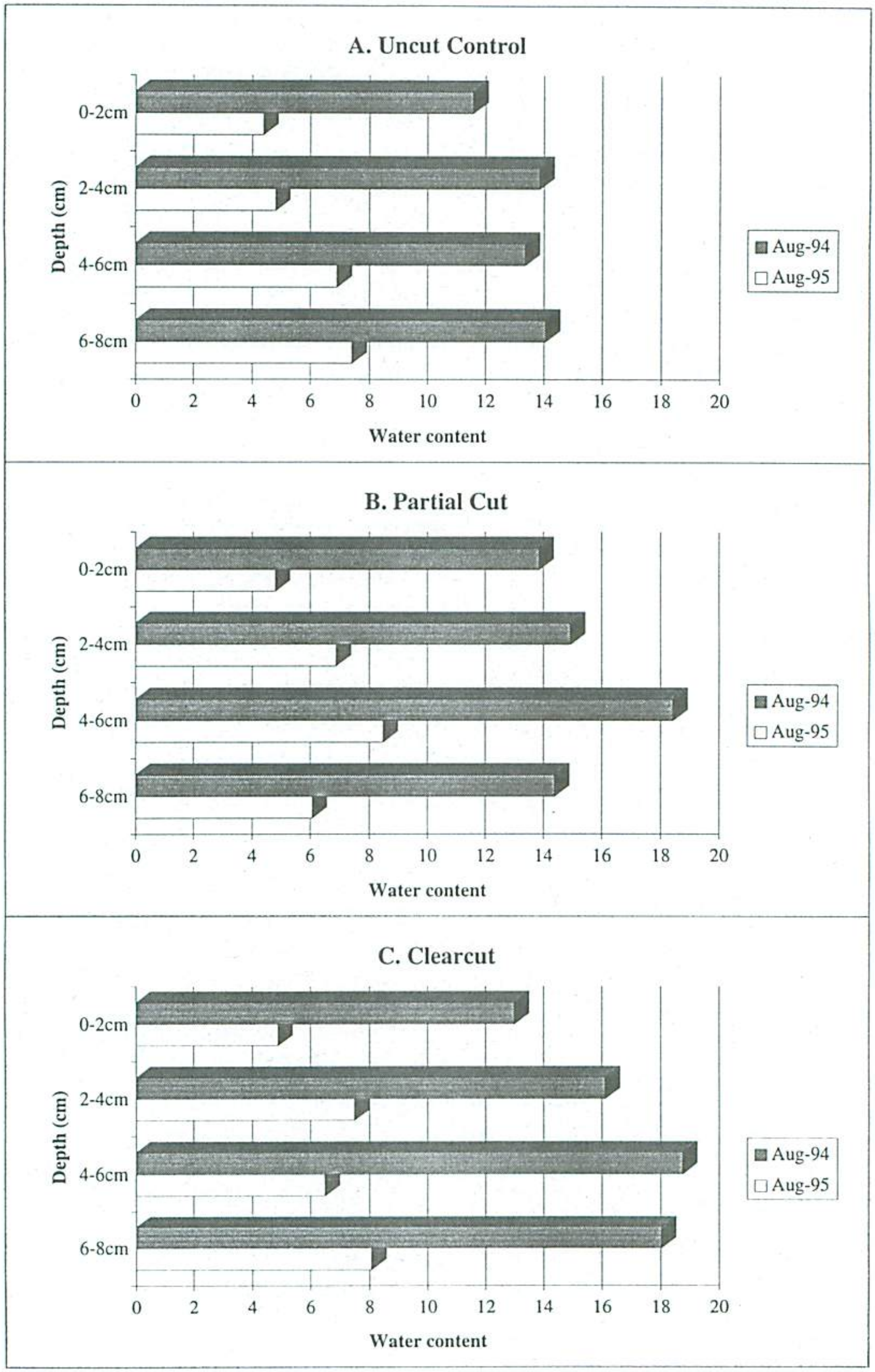

Figure 3. Water content of soil samples (g water/60 cc soil) taken in August 1994 and August 1995. A. uncut control; B. partial cut; C. clear-cut.

Table 13. Comparison of capture rate of carabids (standardized as no./100 trapnights) in August 1994 and August 1995. 2-way ANOVA indicated no significant differences.

Treatment	Number. of replicates	Capture rate ± SE	
		1994	1995
Uncut controls	3	8.9 ± 0.5	7.9 ± 1.0
Partial cuts	3	6.2 ± 1.4	8.5 ± 1.0
Clear-cut A	3	5.3 ± 2.0	9.8 ± 1.0

Table 14. Comparison of population numbers for dipteran larvae in August 1994 and August 1995. 2-way ANOVA indicated significant time (P<0.001) and treatment (P<0.001) effects, and a significant time x treatment interaction (P=0.03). Within one time period, means not followed by the same letter differ significantly from one another (Bonferroni t-tests, P<0.05).

Treatment	Number of replicates	Mean number of individuals ± SE /m^2		time within treatment comparison P<0.05
		1994	1995	
Uncut controls	6	1 827 ± 511 a	724 ± 90 b	No
Partial cuts	3	1 134 ± 608 a	189 ± 109 ab	Yes
Clear-cut	5	1 209 ± 386 a	38 ± 38 a	Yes

Table 15. Comparison of population numbers for mites in August 1994 and August 1995. 2-way ANOVA indicated no overall significant time (P=0.061) or treatment (P=0.326) effects, but there was a significant time x treatment interaction (P=0.01). Within each time period, means not followed by the same letter differ significantly (Bonferroni t-tests P<0.05).

Treatment	Number of replicates	Mean number of individuals ± SE /m^2		time within treatment comparison P<0.05
		1994	1995	
Uncut controls	6	176 673 ± 11 372 a	162 558 ± 23 410 a	No
Partial cuts	3	90 824 ± 17 256 b	217 109 ± 32 987 a	Yes
Clear-cut	5	144 740 ± 13 058 ab	136 387 ± 23715 a	No

Table 16. Comparison of population numbers for Collembola in August 1994 and August 1995. 2-way ANOVA indicated a significant time effect (P=0.002), but treatment (P=0.427) and the time x treatment interaction (P=0.983) were both not significant.

Treatment	Number of replicates	Mean number. of individuals ± SE /m^2	
		1994	1995
Uncut controls	6	58 859 ± 13 016	27 807 ± 7 311
Partial cuts	3	37 350 ± 6 494	19 141 ± 7 095
Clear-cut	5	53 457 ± 9 384	28 910 ± 9 875

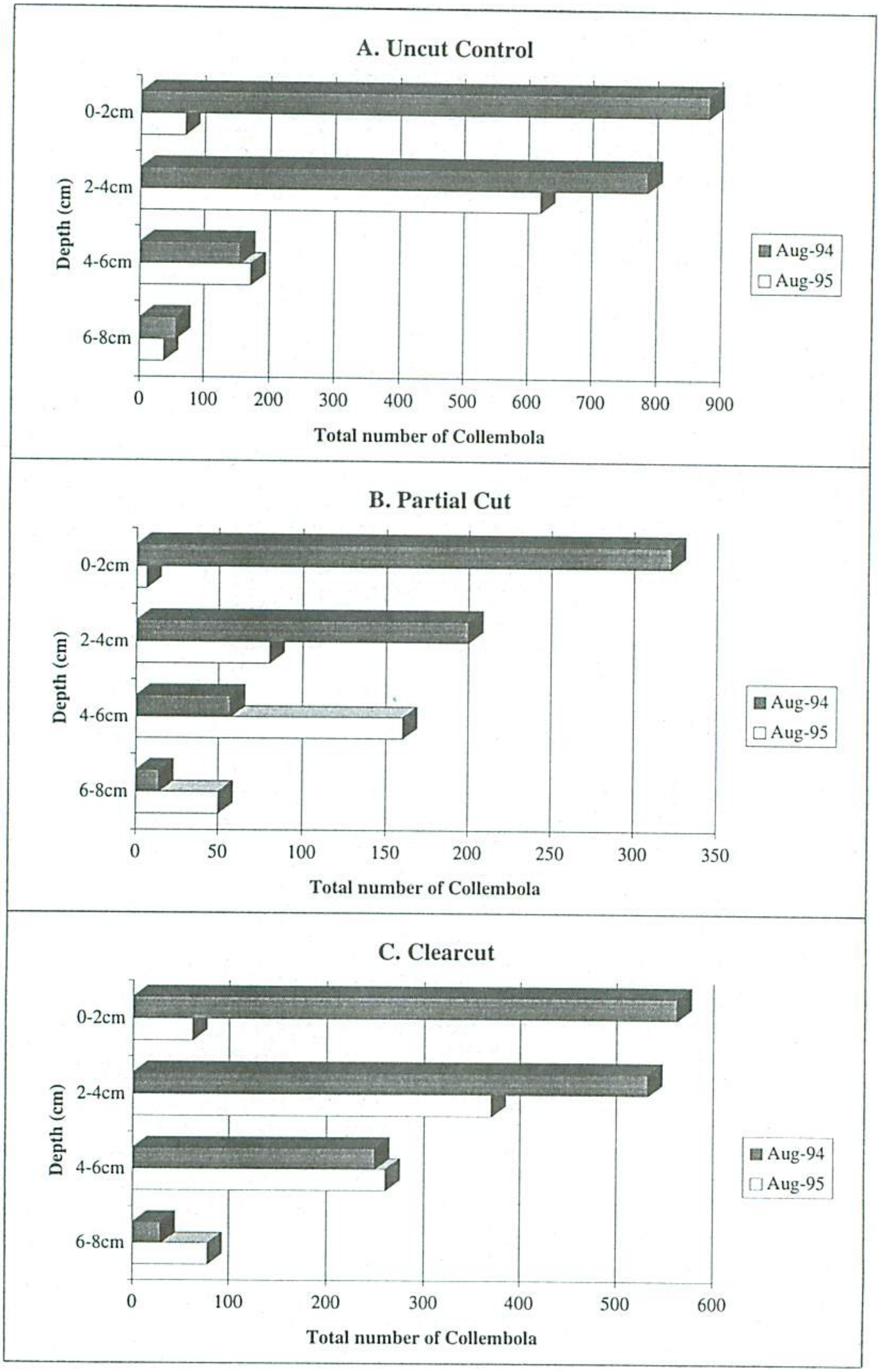

Figure 4. Comparison of depth distribution of Collembola in August 1994 and August 1995. Total numbers of Collembola (pooled data from all samples in all replicates of each treatment are shown). A. uncut control; B. partial cut; C. clear-cut.

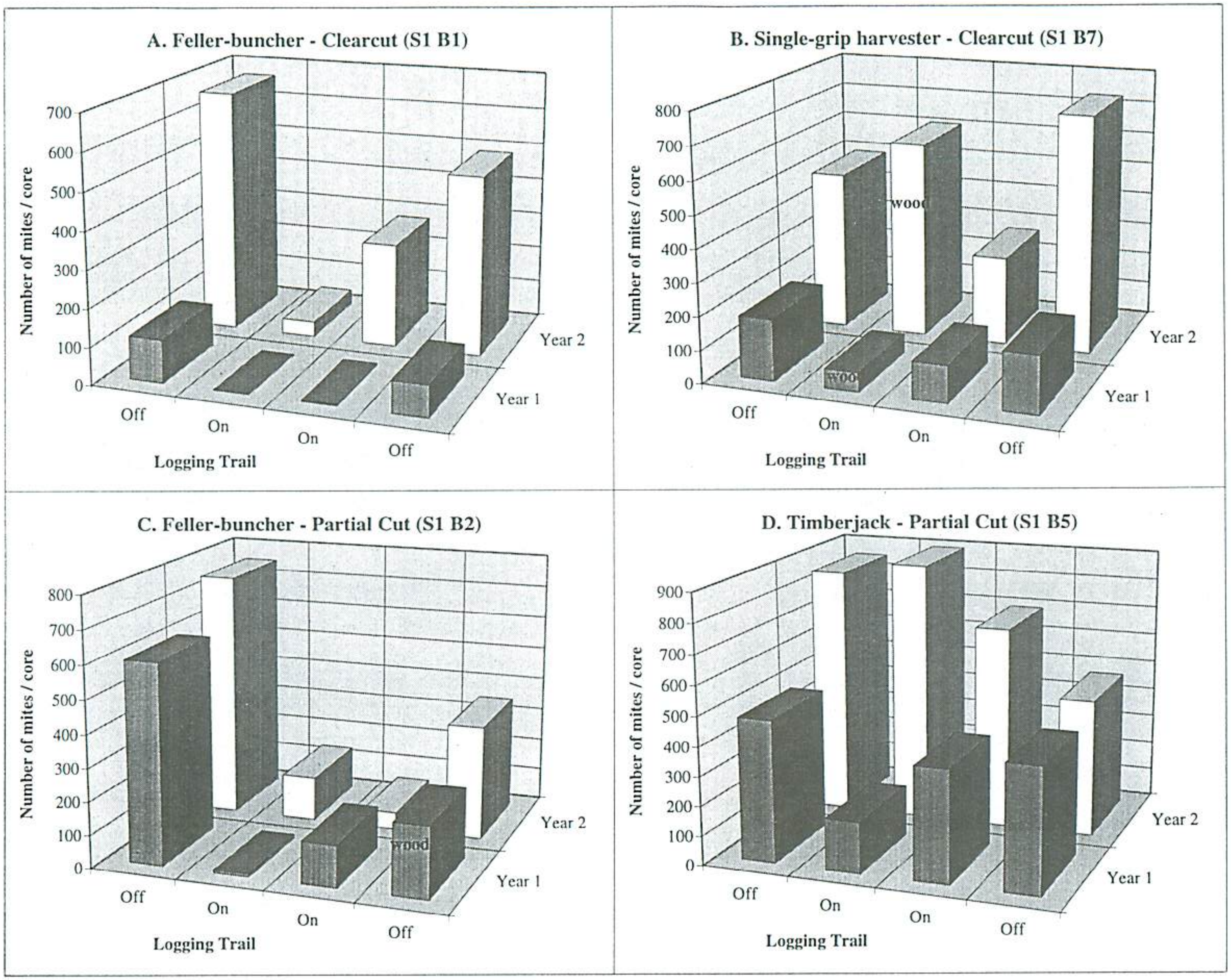

Figure 5. Abundance of mites in cores taken across logging trails. The first and last cores were taken in the undisturbed soil beside the trail, the two middle cores were taken on the trail, 2 m from the edge. A. feller-buncher - clear-cut (S1 B1); B. single-grip harvester - clear-cut (S1 B7); C. feller-buncher - partial cut (S1 B2); D. timberjack - partial cut (S1 B5).

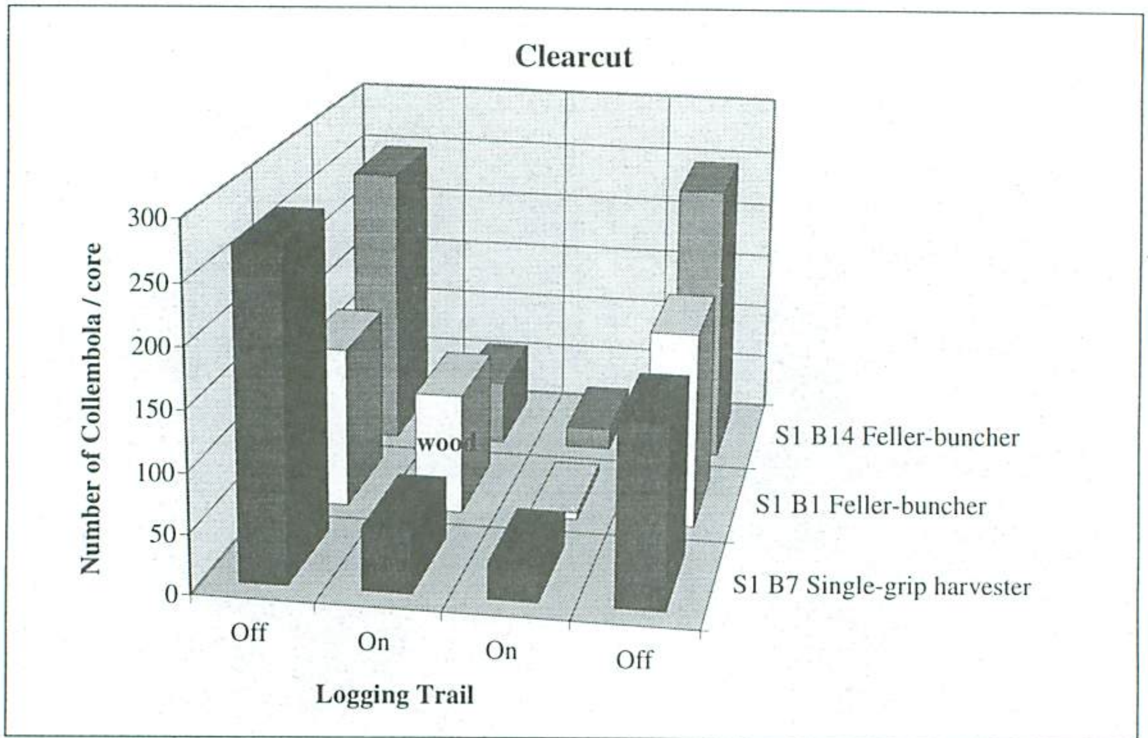

Figure 6. Abundance of Collembola two years post-harvest in cores of soil taken across logging trails on clear-cuts. The first and last cores were taken in the undisturbed soil beside the trail, the two middle cores were taken on the trail, 2 m from the edge.

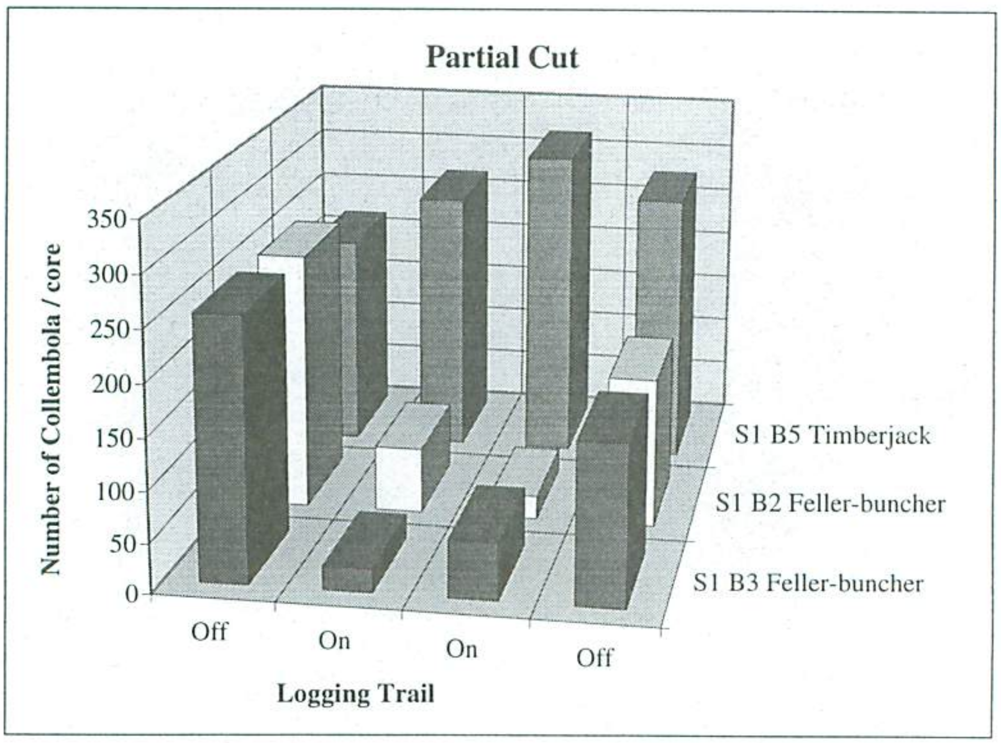

Figure 7. Abundance of Collembola two years post-harvest in cores of soil taken across logging trails on partial cuts. The first and last cores were taken in the undisturbed soil beside the trail, the two middle cores were taken on the trail, 2 m from the edge.

and feller-buncher harvesting regimes in both years were lumped. The analysis indicated that on logging trails, there were significantly more mites (t=4.383, D.F.=3, P=0.022) and Collembola (t=3.464, D.F.=3, P=0.041) in samples containing wood, than in those without wood. There were insufficient data to attempt a similar comparison for partial cut logging trails.

DISCUSSION

The high variability in the distribution and abundance of soil fauna, combined with low numbers of replicates means that the power of the statistical tests was generally low. Consequently the fact that in many cases differences were not significantly different, needs to be interpreted with caution.

Different groups of the soil fauna responded in different ways to the different harvesting regimes.

Seasonal abundances of larval Diptera (two years post-harvest) and mites (one year post-harvest) were affected by the different harvesting regimes, with both groups showing lower numbers on clear-cuts. An initial decrease in mite abundance on clear-cuts was also reported by Bird and Chatarpaul (1986) in a red pine (*Pinus resinosa* Ait)/ aspen (*Populus* spp.)/white pine (*Pinus strobus* L.) mixedwood forest near Petawawa Ontario, and in a comparison of cut and uncut Norway spruce (*Picea abies* [L.] Karst.) stands in Finland (Huhta 1976; Huhta et al. 1967, 1969).

In the present study, total numbers of Collembola were unaffected by harvesting. In contrast, Bird and Chaterpaul (1986) reported a decline in collembolan numbers on clear-cuts harvested by whole-tree logging, although they found no significant effect in the conventional harvest plot (stems <9 cm dbh not harvested, all slash left on site). As in the present study, Huhta (1976) reported no significant effect of clear-cutting on collembolan numbers in northern Finland in the first few years (two and five years) post-harvest, although numbers started to decline in the longer term (12 years). In southern Finland, collembolan numbers increased immediately post-harvest before starting to decline 5–6 years later.

This study indicated no significant effect of the experimental harvesting treatments on total catches of carabid beetles. Duschene and McAlpine (1993), working in stands of jack pine, were also unable to detect statistically significant differences among the numbers of carabids captured on clear-cuts, burned sites, and uncut controls. Niemalä et al. (1993a) reported that carabid abundance was as high or higher in one- and two-year-old regenerating stands of lodgepole pine (*Pinus contorta* Douglas var. *latifolia* Engelman) and white spruce (*Picea glauca* (Moench) Voss) in northern Alberta, as it was in some of their uncut controls.

It therefore appears that for both Collembola and carabids, counts of the total abundance of these groups do not show a response to harvesting, or, according to the scientific literature, respond in an inconsistent manner. Yet although harvesting impacts on carabids and Collembola were not demonstrated when these taxa were considered at a gross level, harvesting effects were readily shown when examined at the species level.

A total of 10 species of carabid were identified on the uncut blocks in 1994, with 13 species on the partial cuts and 13 species in clear-cut A and 19 species in clear-cut B. The following year, 13 species were taken in traps located in uncut blocks, while the number of carabid species found in the partial cuts had increased to 21, with 23 species on each of clear-cut A and clear-cut B (Figs. 1 and 2). The trend towards increasing species richness on clear-cuts is confirmed by significant increases in the values of N0 from uncut blocks, through partial cuts to clear-cuts. This is thought to be the result of persistence of mature forest generalists coupled with the invasion of cut sites by open-habitat species.

Although species richness in the carabid fauna tended to increase along the gradient from uncut, through partial cuts to clear-cuts, values for species diversity (N1 and N2) and species evenness decreased along the same gradient. This same phenomenon is seen in the study by Duchesne and McAlpine (1993), who demonstrated a reduction in diversity (Shannon-Wiener index) on clear-cut blocks compared to uncut forests, although in their case, species richness in the clear-cuts (mean=11.3 species) was not significantly higher than in the uncut forest (mean=4.1 species). Niemalä et al. (1993a) also found a higher species richness in regenerating stands. They also suggest that assemblages of carabids from mature forests are dominated by fewer species, while carabid abundance is more evenly distributed in regenerating stands. This result is in stark contrast to our study where there was a decided dominance of *P. adstrictus* on partial cuts and clear-cuts one and two years after harvest, while the assemblages in uncut forests are more appropriately described as co-dominant. Nonetheless, Niemalä et al. (1993a) indicate that increases in the catches of both *P. adstrictus* and *P. decentis* in cut areas were implicated in the decrease in the degree of similarity between the carabid faunas of the cut and uncut forest in the season following a winter harvest. Although the results for *P. adstrictus* mirror those in our study, the response of *P. decentis* is the reverse (Table 10).

Pterostichus adstrictus can be described as a generalist with the capability of establishing and expanding local populations in a wide range of habitats. Goulet (1974) studied the biology of *P. adstrictus* and *P. pensylvanicus* in Alberta, and found that compared with *P. pensylvanicus*, *P. adstrictus* began ovipositing earlier in the spring, laid 1.5 times as many eggs and the eggs, larvae and pupae developed faster. The wider range of substrate acceptance by ovipositing *P. adstrictus* could expose eggs to higher mortality rates in dry seasons, but under favourable conditions, a rapid colonization of new resources and habitats could be expected. *P. pensylvanicus* had a narrower range of oviposition substrate acceptance (Goulet 1974), preferring the wettest substrates. There does not appear to have been a noticeable negative effect of the drought conditions in the summer of 1995 in the study reported here but effects related to reproductive success would not have been reflected until the following season.

The species of *Harpalus*, which came to prominence in the second year post-harvest, are known to be "most abundant in open, dry country, usually on sandy soil" (Lindroth 1968). In the present study, they were concentrated on the clear-cut blocks (Table 11). Adults of these species are known to be mostly vegetarian and may be taking advantage of a profusion of herbaceous growth in these open areas, where they are likely to have a continuing presence.

Calosoma frigidum was collected mainly from partial cuts and uncut control blocks. These very capable fliers (Lindroth 1961) may be responding to irruptions of arboreal caterpillar prey (such as *Choristoneura fumiferana* (Clem.), *Choristoneura conflictana* (Wlk.), *Malacosoma disstria* Hbn., and *Enargia decolor* (Wlk.)). This would lead to a concentration of activity in this species, which tends to be cyclical in its population fluctuations (Crins 1980), on these blocks with standing trees.

In the first year post-harvest, comparing equal numbers of blocks (Stands 1 and 2 only, comparable to the pitfall trap sites), 37 species of Collembola were identified from the uncut forest blocks, compared with 34 on the partial cuts and 28 on the clear-cuts. The following year (based on spring and summer samples only), species richness was similar in all treatments (28 species on uncut blocks, 26 species in the partial cuts, and 29 species on the clear-cuts). With the exception of three species, (each with total catches of less than five individuals/species), all the collembolan species found on the clear-cut and partial cut sites during the two years of study were also found in the uncut controls or in the preharvest samples. Since Collembola are flightless, extremely sensitive to desiccation, and have poorly developed dispersal capabilities, rapid immigration of new species would not be expected (Moldenke and Lattin 1990b). Thus, unlike the case for the carabids, even two years post-harvest there was still little evidence of the arrival of species adapted to clear-cut conditions, and no consequent increase in species richness on harvested areas.

Although there was a trend towards lower values for the diversity indices for Collembola on the clear-cuts compared with uncut forests, the difference was statistically significant only for N1 (number of abundant species) in the first year post-harvest. The collembolan fauna of the study blocks was extremely variable, with several species showing extremely aggregated distributions. For example, while the mean number of Collembola /core was about 150 individuals, during the post-harvest study ten cores contained more than 150 individuals of a single species. These samples had a great influence on the calculated values for the diversity indices. Seven of the ten cores with such "abnormally" high numbers of a single species (which tended to reduce values of N1 and N2) were obtained from uncut control blocks. One of the most aggregated species was a *Ceratophysella* sp. (probably *pseudarmata*) with up to 750 individuals in a single core. During the post-harvest study, all three cores that contained over 150 individuals of this species were taken from control sites. However, given the extremely patchy occurrence of this species, it is only possible to speculate that its distribution might be affected by clear-cutting. In the preharvest samples, *Ceratophysella* sp. (probably *pseudarmata*) was also found to occur in large aggregations in blocks that were later clear-cut. On the other hand, large aggregations of *Folsomia nivalis* (Packard) were found on harvested and uncut sites. Thus, although diversity indices give information about the pattern of relative species abundance, they do not take into account which species are contributing to the index. This important shortcoming in the usefulness of diversity indices for describing and evaluating biodiversity was also noted by Freedman et al. (1994).

In the dry summer of 1995, collembolan numbers were reduced across all treatments, including the uncut forests. This reduction in abundance was not demonstrated by the mite populations, neither were capture rates of carabid beetles reduced from values obtained the previous year.

Cancela da Fonseca et al. (1995) suggested that Collembola and mites differed in their response to soil moisture, with Collembola (most of which rely on cutaneous respiration) responding positively to higher levels of soil moisture. Moisture levels and collembolan numbers were indeed greatly reduced in all treatments in the upper soil layers (0–2 cm and 2–4 cm) in the 1995 summer samples. Although moisture was also reduced in the 4–6 cm depth, there was no corresponding decrease in the collembolan fauna. High temperatures, and the interaction between moisture and temperature undoubtedly influenced the distribution and abundance of Collembola.

Population numbers of dipteran larvae were also affected by the drought, but in this case, a significant decrease in abundance was only detected on partial cuts and in clear-cuts. Abundance in the uncut forest was unaffected. The numbers of dipteran larvae in the soil depends not only on the prevailing soil conditions, but also on the response of the adult stages to above-ground conditions. Clear-cuts typically show increased wind speeds and decreases in RH compared with uncut forests, which may help to explain why dipteran larval numbers were so sensitive to the effects of harvesting.

The boreal mixedwood forest is a fire-dominated ecosystem. In the study area, the historical fire frequency is about 50–100 yr (Alexander and Euler 1981). Consequently, the soil faunal community has evolved in an environment where relatively large changes in the structure and composition of the above-ground vegetation, in soil micrometeorological conditions, and in the quality and quantity of litter inputs can be expected to occur. Many of the same general types of changes will also occur as a result of clear-cutting, so that many of the adaptations which allow organisms to survive in a fire-dominated system will also be of significance in dealing with the environmental changes that occur as a result of harvesting. The dominant carabid species in the study, *P. adstrictus*, shows many life history traits that are advantageous under clear-cut conditions (Goulet 1974). Laboratory experiments with *F. nivalis*, the most abundant collembolan species at all the study blocks, have shown that given adequate temperature and moisture conditions, populations of this species, maintained in field-collected litter without additional food, were able to increase 50-fold over 8 weeks (Addison 1996). This "r-selected" species is obviously well adapted to respond quickly to favourable conditions, even if resources can only be exploited during a relatively brief period of time. Many of the other collembolan species present in the natural community are apparently parthenogenic, an adaptation well suited for the rapid exploitation of resources, such as increased availability of food in the form of dead roots, or debris left onsite following harvesting.

The preliminary study of the effects of logging trails on microarthropods indicated that very little damage occurred on the trail left by the Timberjack in Partial Cut Block 5. The results of the present study need to be considered in conjunction with other studies carried out at the sites to evaluate more fully the potential of this technology in partial cutting systems.

CONCLUSIONS AND MANAGEMENT IMPLICATIONS

There is no doubt that soil invertebrates are affected by harvesting practices. Although effects of harvesting were reflected in the overall abundance of such groups as mites and dipteran larvae, effects on carabid beetle populations and Collembola were detected only at the species level.

In the case of the carabids, the fauna respond by the addition of new species in the clear-cuts, and shifts in the proportional representation of the species already present. As yet there is no strong evidence for loss of carabid species in the harvested blocks. The three species that were not captured in 1995 were rarely collected in 1994 and were never taken from control blocks. Their absence in 1995 may be the result of the vagaries of sampling. The major response of the collembolan fauna to harvesting was shifts in the relative abundance of the different species. Several species of Collembola found in uncut blocks were not collected in clear-cut samples, but these were all rare species, and may simply have been missed. Further research will be required to confirm their absence under clear-cut conditions. In the case of the Collembola, the natural stress imposed by the hot dry summer had a far greater impact on the fauna than the harvesting treatments.

In designing forest management strategies in which consideration is given to conserving the natural diversity of the boreal mixedwood soil fauna, the following points should be considered:

Characteristics of the Soil Fauna of Boreal Mixedwood Forests

1. The soil fauna in the boreal mixedwood forest is very diverse. At present, because of our lack of understanding about the ways in which different species contribute to the functioning of the soil system, it is best to operate on the principle of retaining as many of the species as possible. As Freedman et al. (1994) point out, this is not the same as blindly maximising biodiversity. In the present study, the fauna of the clear-cuts was still diverse, but the composition was different than in the uncut areas. As Freedman et al. recommend *"if forestry is to be practised in an ecologically sustainable fashion, then all elements of biodiversity must be accommodated within a landscape."* (Freedman et al. 1994)

2. In soils with a mor-type humus, such as boreal mixedwood and coniferous forest soils, the overwhelming majority of the soil fauna is confined to the organic horizons (Petersen and Luxton 1982). At the present study site, a series of 10 preharvest samples showed that only 2.3 percent of the total number of Collembola were found below the organic/mineral soil interface.

3. The soil fauna of boreal forests must be able to adapt to major disturbances such as drought and forest fires. In the present study, the natural drought seemed to have more of an impact on collembolan abundance than the harvesting.

4. Harvesting effects on soil invertebrates are expressed at the species level and may not be detected in studies that deal only at gross taxonomic levels.

Management Implications

1. *Use harvesting techniques that minimize soil compaction and damage to the organic layer.*

Soil compaction due to logging activities, and removal of the organic mat (either as a result of harvesting or site preparation activities) have been identified as major factors contributing to declines in forest productivity (Powers et al. 1990, Baker and MacKinnon 1990, Utzig and Walmsley 1988). In northern boreal forests, most of the nutrients and the bulk of the soil fauna are found in the organic mat. Where some removal of the organic material is required (e.g., for the establishment of coniferous seedlings) a number of techniques to limit the disturbance to "microsites" have been suggested for northern Ontario soils (Sutherland and Foreman 1995).

In the present study, use of the Timberjack appeared to cause little (if any) damage to the organic mat or its resident invertebrate populations. On the other hand, use of this machinery in the boreal mixedwood forest has been criticized because it does not permit operators to remove some of the advanced fir growth in the stand during the harvest.

2. *Avoid creating situations of microclimatic extremes.*

Under natural conditions, boreal soil invertebrates have to deal with major perturbations in their environment so some degree of tolerance to changes in the physical environment can be expected. However, many soil invertebrates are extremely sensitive to temperature and moisture extremes. The clear-cuts in this study were about 10 ha in size, fairly small by operational standards. Limiting the size of clear-cuts, or the use of partial cuts reduces microclimatic extremes. In general in this study, microclimatic and biological variables (e.g., diversity indices) determined for the partial cuts were intermediate between values obtained for the uncut forests and the clear-cuts.

3. *Regenerate boreal mixedwoods as mixed woods.*

Although in the past, traditional forestry practices favoured the establishment of simple stand structures that produced coniferous wood, there is growing scientific and political support for managing the boreal mixedwood resource as mixed species forests. (Kimmins 1995, MacDonald 1995, 1996, Weingartner 1996).

Mixed litters, particularly when litter with a relatively high nutrient content is mixed with a low-quality litter, have been shown to enhance soil nutrient status (Navratil et al. 1991, Nyyssonen 1991). In their study of decomposition and nutrient release in mixed and single species plantations, Chapman et al. (1988) concluded that part of the explanation for modified tree growth in mixed compared with pure stands was due to the interactions between soil invertebrates and microorganisms in the litter, which resulted in changes in nutrient dynamics. Improved control of fungal diseases as a result of the feeding activities of soil invertebrate communities associated with multispecies planting were reported by Kessler (1990). Where only the litter of a single tree species was present, suppression of the pathogenic fungus did not occur.

4. *Provide refugia from which re-colonisation of cut areas can occur.*

It will be important to maintain refugia from which re-colonisation can take place, particularly in the case of small, fragile invertebrates, which lack well developed dispersal capabilities. These refugia would include, at the landscape level, tracts of uncut forest and at a microsite scale, coarse woody debris and areas of intact forest floor.

Woody debris provides nutrients, and an added dimension of structural diversity for soil invertebrates. In particular, decomposing woody debris provides islands of habitat and food, and protection from microclimatic extremes, permitting species to maintain a foothold in temporarily inhospitable environments. Koponen (1995) suggested that the rapid re-appearance of certain soil microarthropods in burnt areas one year after a fire, was best explained by their survival in refugia within the burn area rather than by colonisation from the surroundings. The same principle probably holds for clear-cuts. In the present study, on clear-cuts, the presence of decomposing woody debris on logging trails appeared to mitigate the adverse effects of the harvesting machinery on soil invertebrate populations.

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Appendix A

Species of carabid beetles abbreviated in Figures 1-2.

Pterostichus adstrictus Eschscholtz
Calathus ingratus Dejean
Pterostichus pensylvanicus LeConte
Sphaeroderus nitidicollis brevoorti LeConte
Platynus decentis (Say)
Agonum retractum LeConte
Scaphinotus bilobus (Say)
Pterostichus punctatissimus (Randall)
Synuchus impunctatus (Say)
Poecilus lucublandus lucublandus (Say)
Pterostichus coracinus (Newman)
Harpalus fulvilabris Mannerheim
Harpalus solitaris Dejean
Cymindis cribricollis Dejean
Agonum placidum (Say)
Notiophilus semistriatus Say
Pterostichus melanarius (Illiger)
Carabus serratus Say
Harpalus laticeps LeConte
Amara erratica (Duftschmid)
Syntomus americanus (Dejean)
Bembidion rapidum (LeConte)
Badister obtusus LeConte
Calosoma frigidum Kirby
Harpalus innocuus LeConte
Agonum cupripenne (Say)
Bembidion mutatum Gemminger & Harold
Bembidion quadrimaculata oppositum Say
Harpalus laevipes Zetterstedt
Harpalus somnulentus Dejean
Bradycellus lugubris LeConte
Sericoda quadripunctata (DeGeer)
Bembidion grapii Gyllenhal
Bembidion wingatei Bland