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Chemical constituents of vole feces as indicators of bark use in sapling plantations

Jean-Marie Bergeron

Bergeron, J.-M., Groupe de Recherche en Écologie, Nutrition et Énergétique, Département de Biologie, Faculté des Sciences, Université de Sherbrooke, 2500 boulevard Université, Sherbrooke, Québec, Canada, J1K 2R1

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Population density of meadow voles (*Microtus pennsylvanicus*) and amount of bark removal of conifer and deciduous seedlings were estimated in a young meadow and in an old-field community used as tree plantations. Vole feces were sampled to assess the changes in neutral detergent solubles, total phenolics, total non-structural carbohydrates, and protein from fecal matter. In 1992, voles reached peak densities with similar population characteristics in both meadows. This was followed in the spring 1993 by bark removal on deciduous seedlings in the young meadow and on wild shrubs (not spruce trees) in the old-field community. Chemical components measured in the fall 1992 feces contained significantly more phenolics and carbohydrates than fall samples collected the year after peak density. Fecal matter from voles trapped in the young meadow in the spring of 1993 contained high levels of phenolics and carbohydrates after the winter use of bark tissues. Chemical analyses of fecal matter may be useful in predicting the nutritional status of voles in tree plantations before bark removal, and might be developed as a tool to aid in management of rodent populations.

1. Introduction

Fecal droppings can be used to provide a rapid analysis of the nitrogenous content of forage for ruminants (Hinnant & Kothmann 1988). Strong relationships exist between fecal nitrogen and digestibility or intake of forage for domestic or wild ruminants (Mabanga *et al*. 1985, Renecker & Hudson 1985). For non-ruminant mammals, such as snowshoe hares (*Lepus americanus*) (Sinclair *et al*. 1982, 1988) and pocket gophers (*Thomomys bottae*) (Loeb & Schwab 1989), protein content of feces is highly correlated with protein levels of diet ($r = 0.96$ and 0.94, respectively). This suggests that the feces of some small mammals may also be useful in following nitrogen variations in the diet. Feces are also of some use to field biologists for rapid diagnosis of quality of food intake (Cranford & Johnson 1989), or predicting population density of voles living in agroecosystems (Delattre *et al*. 1990). Vole feces could perhaps be indicative of food use switches occurring in young sapling plantations prior to seedling losses after bark use by voles. In Québec, Canada, young deciduous tree plantations are dispersed over a territory of

680 000 km^2. Standard trapping methods to follow small rodent population cycles cannot be used on such a large scale when foresters want to know precisely where and when to apply protection measures against rodents. Feces collection and chemical analyses of fecal matter could perhaps be easier to perform for this purpose if they can yield enough information on the nutritional status of the target species.

Meadow voles (*Microtus pennsylvanicus*) maintained in fenced grids developed extremely high population densities during the summer (Bergeron & Jodoin 1993), with quality of ingested food decreasing and remaining low during the following winter (Bergeron & Jodoin 1995). Vole feces also showed during winter high values of protein, total nonstructural carbohydrates, and total phenolics in the most crowded plots where animals were using bark as alternate food. These chemical constituents from vole feces could perhaps be used as indicators of low-quality food use before loss of bark tissues occurs. An opportunity was provided to test this hypothesis when two vole populations peaked in densities in the summer 1992, one in a deciduous plantation and the other in a conifer tree plantation. Population densities had been followed since 1991, and feces had been collected in the spring and fall of each year. Voles from these plots severely girdled the introduced seedlings on one plot and wild shrubs on the other.

Meadow voles can use extensively bark tissues in plantations (Von Althen 1979, Ostfeld & Canham 1993) despite the fact that bark of coniferous trees yield lower nutritional values than the remaining herbaceous green plants in winter (Bucyanayandi *et al*. 1992). For reasons not fully understood, voles living under crowded conditions often supplement their normal leaf diet in winter with bark and cambium tissues of young trees (Baumler 1975, Hansson 1985, Pigott 1985). Bark of many conifer species has low protein and carbohydrate contents and high concentrations of total phenolics. By comparing these parameters from vole feces collected at low and high population density, in a young and old-field community used as a plantation site, I aimed to predict which variable(s) differ significantly before heavy bark losses occur. My hypothesis is that vole feces collected during a summer peak population density will yield significantly more phenolics, carbohydrates and neutral detergent solubles than feces sampled from lower density stages.

2. Materials and methods

Fecal droppings of meadow voles were collected twice a year, between 1991 and 1993 in the spring (end of April) and fall (end of August). Dropping boards (10 × 10 cm masonite) were placed in shelters on an 8-year old Norway spruce (*Picea abies*) plantation which was established in an old-field community and on a new plantation of red oak (*Quercus rubra*) and white ash (*Fraxinus americana*) introduced in a young meadow reclaimed from agriculture. The 3-ha plot of coniferous saplings was divided into a 7.5 × 15 m grid pattern with 350 collecting stations, while the 0.33 ha plot of deciduous seedlings was divided into a 5 × 5 m grid pattern with 120 stations. The grid pattern on the old-field habitat was more extensive in order to make a compromise between the 10 × 10 m and 15 × 15 m sampling intervals normally used in typical vole grasslands or older field habitats (Banach 1987, Parmenter *et al*. 1987, Kennedy *et al*. 1989). Fecal matter at each station was collected in plastic bags and frozen to – 20°C until analysis.

Indices for seedling or young tree damage were established in the spring of each year (1991–1993) following a modified procedure from Hansson (1985):

0 – no damage registered on stems;
1 – less than 25% of the stem circumference girdled;
2 – between 25 and 50% girdled;
3 – between 50 and 75% girdled;
4 – between 75 and 100% girdled.

Bark use indices were almost identical for the oak and ash seedlings; since an equal number of both species had been planted in the young meadow, we used a mean index value for this plot. Population density of meadow voles was sampled in spring and early fall after each collection of fecal droppings. Sherman live traps were located at each station of the grid pattern and prebaited with peanut butter for 2 days prior to trapping and used with cotton as bedding material for 4 consecutive nights at each trapping session. Each animal was individually toe clipped to estimate the minimum number of voles alive (MNA, Taitt & Krebs 1985). The presence of heavy adults (males > 43 g; females > 40 g) was registered in each plot because this is one of the main characteristics of peak populations (Boonstra & Krebs 1979).

Samples of fecal matter were dried in a forced-air oven at 60°C for 48 hrs, weighed and ground prior to analysis. Chemical constituents were analysed in duplicates. A priority order was given to chemical analysis to perform the most informative ones first. Total phenolics were measured using colorimetric procedures (absorbance read at 765 nm) with gallic acid as the standard and Folin-Ciocalteu as the reagent (Singleton & Rossi 1965). Total nonstructural carbohydrate (TNC) determinations followed the technique of Da Silveira *et al*. (1978) using amyloglucosidase (Sigma Chem. Co.) for digestion. After enzymatic digestion, hydrolysis of carbohydrates into monomers was completed with 0.2 N (0.1 M) sulfuric acid (Smith 1969). Neutral detergent solubles (NDS) were evaluated with the procedures of Goering and van Soest (1970). Crude protein content was determined by analyzing total nitrogen and converting the figures into protein (N × 6.25 for plant material: Allen 1976, Maynard *et al.* 1979) using the micro-Kjeldahl method (Lang 1958). Results were expressed as percentages of dry mass.

Nonparametric Mann-Whitney tests were used to compare nutritional contents of vole feces among seasons, years and habitats. χ^2-square contingency tests were performed to compare bark use indices by voles reported through time for each plantation.

3. Results

Population density of meadow voles followed the same fluctuation patterns in both communities. The young meadow contained only graminoïd species, while the old-field habitat harbored 14 shrub species including red osier dogwood (*Cornus stolonifera*), small stems of large-toothed aspen (*Populus grandidentata*), and old-field birch (*Betula populifolia*). In the fall of 1991, both plantations contained only juvenile and subadult voles (data not shown here). At that time, bark use indices were low (Table 1). Seedlings of oak and ash were planted in the young meadow that year. In the spring of 1992, voles reached peak numbers in both plots, with an almost 10-fold increase in density over the fall 1991 levels. In the oak/ash plantation, heavy adult males represented 45% of the spring adult male cohort and 37% in fall, while they varied between 0 and 67% for both seasons in the Norway spruce plantation. Most of the adult cohort of both plots was still reproducing in the fall of 1992 (oak/ash: 22/28; spruce: 2/3). By the spring of 1993, vole numbers had decreased by two thirds in both plots. Spring populations of the oak/ash plantation contained a majority of heavy males (82%) and most of these adults (83%) had started to reproduce. In the spruce plantation, heavy males had disappeared, although most adult males and females (83%) were reproducing. The fall 1993 populations of both plots were once again composed of juveniles and subadults.

Bark use by voles was particularly noticeable in the oak/ash plantation. Twenty-three percent of oak and ash seedlings were used to some degree during the first winter that was characterized by a rapid population increase (Table 1). The bark tissues of seventy-five percent of the seedlings was lost by spring 1993, after the 1992 summer peak density. Bark use indices were significantly different between both years ($\chi_4^2 = 77.02$, $P < 0.0001$). More than half of the saplings were completely girdled. The Nor-

Table 1. Density of meadow voles and bark use indices in the oak/ash and spruce seedling plantations.

Vole population phase at feces collection	Oak/ash plantation: Vole density (/ha)	Oak/ash: Bark use indices (%)[a] 0	1	2	3	4	Spruce plantation: Vole density (/ha)	Spruce: Bark use indices (%) 0	1	2	3	4
Spring 1991: Plantation year for oak/ash plantation	NA	100	0	0	0	0	1	95	2	2	1	0
Fall 1991: Insufficient amount of feces for chemical analysis	13						1					
Spring 1992: Feces from the winter increasing density phase (winter 1991–1992)	133	77	10	7	5	1	9	94	2	2	2	0
Fall 1992: Feces from the summer high vole density phase (summer 1992)	310						2					
Spring 1993: Feces from the winter decreasing density phase (winter 1992–1993)	83	25	8	7	7	53	3	97	2	1	0	0
Fall 1993: Feces from the summer low vole density phase (summer 1993)	53						4					

[a] bark use indices after Hansson (1985) = 0 – no damage to stems, 1– less than 25% of stem circumference girdled, 2 – between 25 and 50% girdled, 3 – between 50 and 75%, 4 – between 75 and 100%.

way spruce plantation did not suffer such losses. Bark use indices did not change between low and high vole density years probably due to the low vole numbers registered, even in the peak year. There was evidence that losses of bark tissues occurred on seven shrub species during the winter 1992–1993 (see Appendix for damage indices registered on those species from 20 random quadrats (7.5 × 7.5 m) sampled in the spring of 1993).

Neutral detergent solubles (NDS) of fecal matter followed similar trends on both plots investigated (Fig. 1). Spring 1992 samples obtained from the wintering 1991 animals were significantly higher in NDS than those collected in fall 1992 from the summer peak voles (oak/ash: $U_{5,12} = 78$, $P < 0.0001$; spruce: $U_{4,9} = 48$, $P < 0.05$). There was no seasonal variation in the following year, while both populations were in the decreasing phase. Total phenolics also followed a similar pattern in both plantations. Fecal samples collected in the spring of 1992 contained significantly less phenolics than the fall 1992 samples (oak/ash: $U_{5,12} = 78$, $P < 0.0001$; spruce: $U_{4,9} = 48$, $P < 0.005$), while no seasonal differences were registered in 1993. Total nonstructural carbohydrates (TNC) were significantly lower in the spring of 1992 ($U_{5,12} = 60$, $P < 0.0001$) and 1993 samples ($U_{3,26} = 92$, $P < 0.05$), compared to the fall collections in the oak/ash plantation. In the spruce plot, TNC were also significantly lower in the spring than in the fall of 1992 ($U_{4,9} = 45$, $P < 0.0001$). Fecal matter was not sufficient in 1992 for estimation of nitrogenous contents. Feces collected in the spring of 1993 in both plantations had a protein content similar to those sampled in the fall of 1993. Fecal matter collected from overwintering voles prior to the summer peak density on both plots had a similar pattern in chemical constituents. Neutral detergent solubles were significantly higher while phenols and carbohydrates were significantly lower compared to the fall samples. The pattern was not observed during the second winter, while population densities were decreasing in both plots.

Feces were collected from voles of two habitats that differed not only in their plant composition but also in the types of seedlings used. From bark use indices of seedlings (Table 1) or wild shrubs (Appendix), there is evidence that voles used bark in both plots. The question arising from this is "can chemical constituents of vole feces yield the same results when sampled in two different habitats with similar population density characteristics?" Fecal samples collected from voles in the old-field community yielded significantly more neutral detergent solubles in the fall samples of the peak year (Fig. 2a) ($U_{4,12} = 65$, $P < 0.0001$) and in the spring samples following the peak density ($U_{15,26} = 426$, $P < 0.0001$) when compared to those collected in the oak/ash plantation. Phenolic contents did not follow this pattern (Fig. 2b), but carbohydrates (Fig. 2c) were significantly higher ($U_{15,26} = 412$, $P < 0.0001$) and protein (Fig. 2d) significantly lower ($U_{15,26} = 352$, $P < 0.0001$) in fecal samples collected from voles in the old-field habitat, the spring after their peak density of 1992.

Most chemical constituents of fecal matter analyzed in this study followed the same seasonal variation for both plantations (Fig. 3). The NDS content of vole feces collected in the spring of 1992, prior to the summer peak density, was significantly higher on both plots than from those estimated from feces of spring 1993, after the peak density (oak/ash: $U_{5,26} = 148$, $P < 0.0001$; spruce: $U_{9,15} = 143$, $P < 0.0001$). However, phenols ($U_{5,26} = 147$, $P < 0.0001$) and carbohydrates ($U_{5,26} = 114$, $P < 0.01$) in fecal samples of the spring of 1992 were significantly lower than those of the spring 1993 samples for the oak/ash plantation only. The opposite pattern was observed in vole feces from fall collections. Phenols (oak/ash: $U_{3,12} = 43$, $P < 0.05$; spruce: $U_{2,4} = 15$, $P < 0.05$) and carbohydrates (oak/ash: $U_{3,12} = 40$, $P < 0.05$; spruce: $U_{2,4} = 15$, $P < 0.05$) were significantly higher in fecal matter sampled from both types of tree plantations during the year of peak density while the NDS contents were significantly lower in the oak/ash samples only ($U_{3,12} = 50$, $P < 0.05$).

4. Discussion

Although fecal droppings collected from dropping boards do not provide individualized information on wild animals, and represent the end products of digesta that is going twice through the gut in the case of coprophagous animals such as meadow voles (Lee & Houston 1993), they are easy to collect in the field, and do not require tight visiting schedules. They could be an asset to nutritional ecologists and foresters if they could yield reliable information on the nutritional status of voles in tree plantations. In young- and old-field meadows used to support deciduous seedlings or conifer saplings, feces of voles

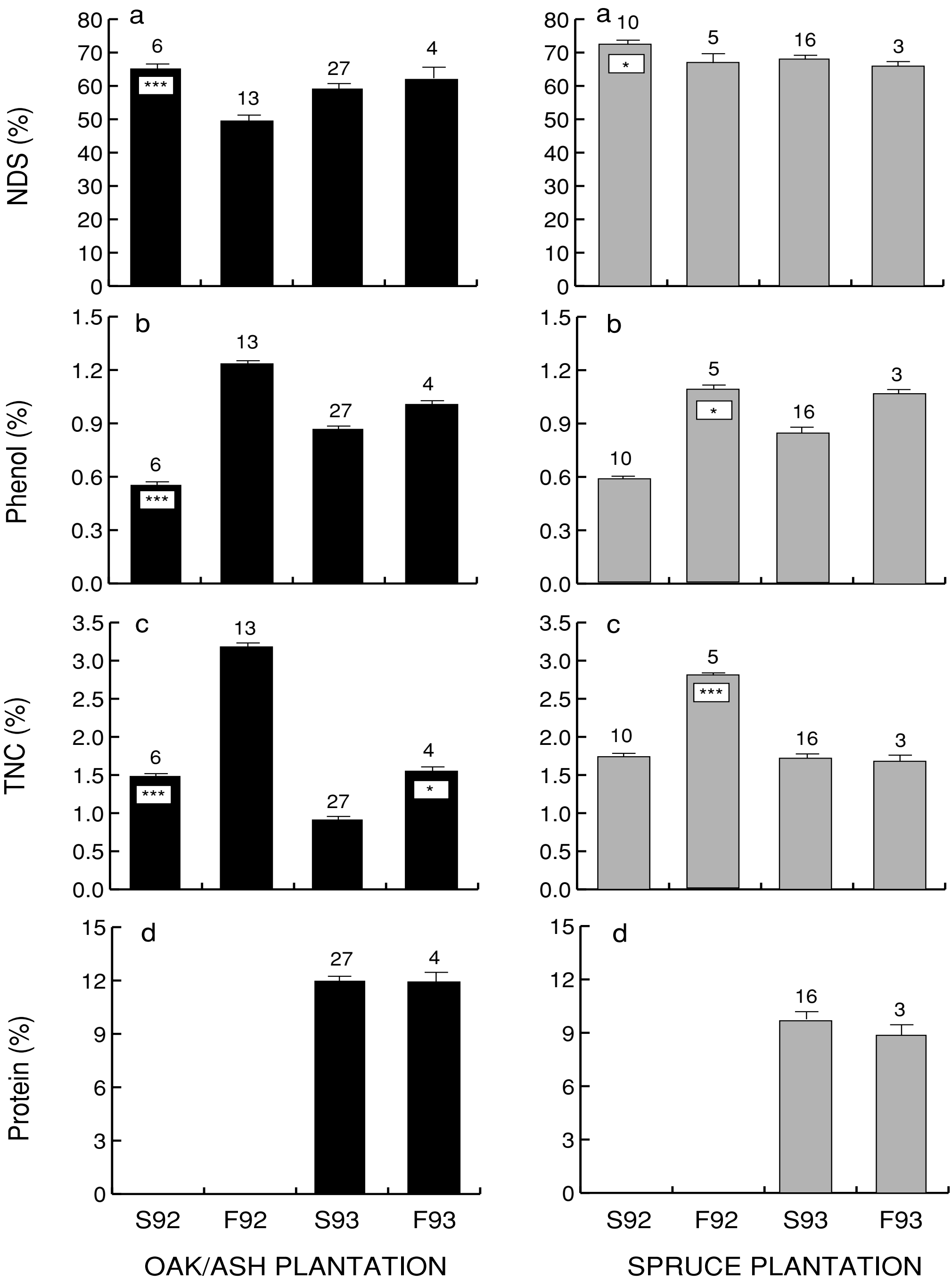

Fig. 1. Variations in composition of fecal matter collected on the oak/ash (left) and spruce (right) plantations during 1992–1993 (*N* above *S.E.* bars). — a: neutral detergent solubles, NDS. — b: phenols. — c: total nonstructural carbohydrates, TNC. — d: protein. Spring (S) and Fall (F). ****P* < 0.0001; ***P* < 0.005; **P* < 0.05, Mann-Whitney tests for paired data.

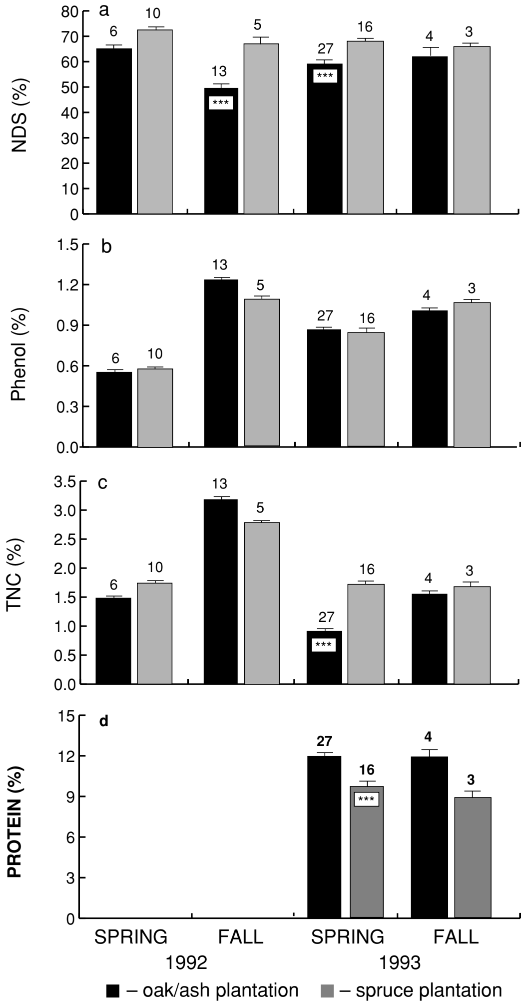

Fig. 2. Inter-plot comparisons of chemical constituents of fecal matter for both years analysed (*N* above *S.E.* bars). — a: neutral detergent solubles, NDS. — b: phenols. — c: total nonstructural carbohydrates, TNC. — d: protein. ***$P < 0.001$, Mann-Whitney tests for unpaired data.

sampled in the fall from populations at peak densities contained significantly more total phenolics and total nonstructural carbohydrates than those collected from animals at lower population densities the following fall (1993). Phenolic contents greater than 1.2% and carbohydrate contents greater that 3% dry mass during the summer, would perhaps be indicative of a low quality diet which will degenerate into bark use the following winter. These events coincided with heavy bark damage of oak/ash seedlings of the deciduous plantation, and in the use of wild shrubs in the older spruce plantation the following winter. In the younger meadow, voles had no alternate food supply available, while several species of wild shrubs were available and were used by voles in the spruce plantation. In a separate study, overwintering voles from fenced plots also yielded fecal matter with phenolic contents > 1.2% dry matter and carbohydrate values > 2.05% dry matter when eating bark tissues (Bergeron & Jodoin 1995).

The preponderance of heavy adults during the peak year was indicative of cyclic populations reaching peak numbers (Taitt & Krebs 1985). With 60% of the seedlings lost after the first peak in vole numbers in the oak/ash plantation, there is a need to develop better management methods to protect young deciduous tree plantations. Young meadows reclaimed from agriculture and used for reforestation are prone to heavy losses of bark tissues (Gill 1992, Ostfeld & Canham 1993) in spite of the fact that such graminoïd-dominated communities should offer optimum cover and food supply. Chemical analyses of fecal matter collected in the young deciduous tree plantation showed significant differences between collections made at different density phases of meadow voles. Spring 1992 fecal samples from voles in the younger meadow were representative of overwintering animals (1991) that experienced no food limitations (low bark damage indices the next spring and low vole numbers the previous fall). The feces showed significantly higher amounts (Fig. 3) of neutral detergent solubles (> 60% dry mass), carbohydrates (> 1.5% dry mass), and lower phenolics (< 0.7% dry masss) over those collected in the spring of 1993, during extensive bark use. Although chemical analyses of vole feces showed a 50% increase in phenolics and a reduction of 25% in carbohydrates in spring 1993, bark losses had already occurred. It was too late to apply protection measures to reduce vole density or bark use in such an habitat. Chemical analyses of feces from fall samples, before girdling occurs would be more appropriate to measure the nutritional status of voles in terms of phenolics and carbohydrates output, and to initiate protective measures to the seedlings.

The pattern of the old-field community was almost identical to that in the younger meadow. Phenolics and carbohydrates from fecal matter were significantly greater in the fall samples of the peak year. As graminoïd-dominated meadows age toward forb/shrub-dominated communities, fluctuations of voles tend to damper (Lidicker 1988), due to a loss

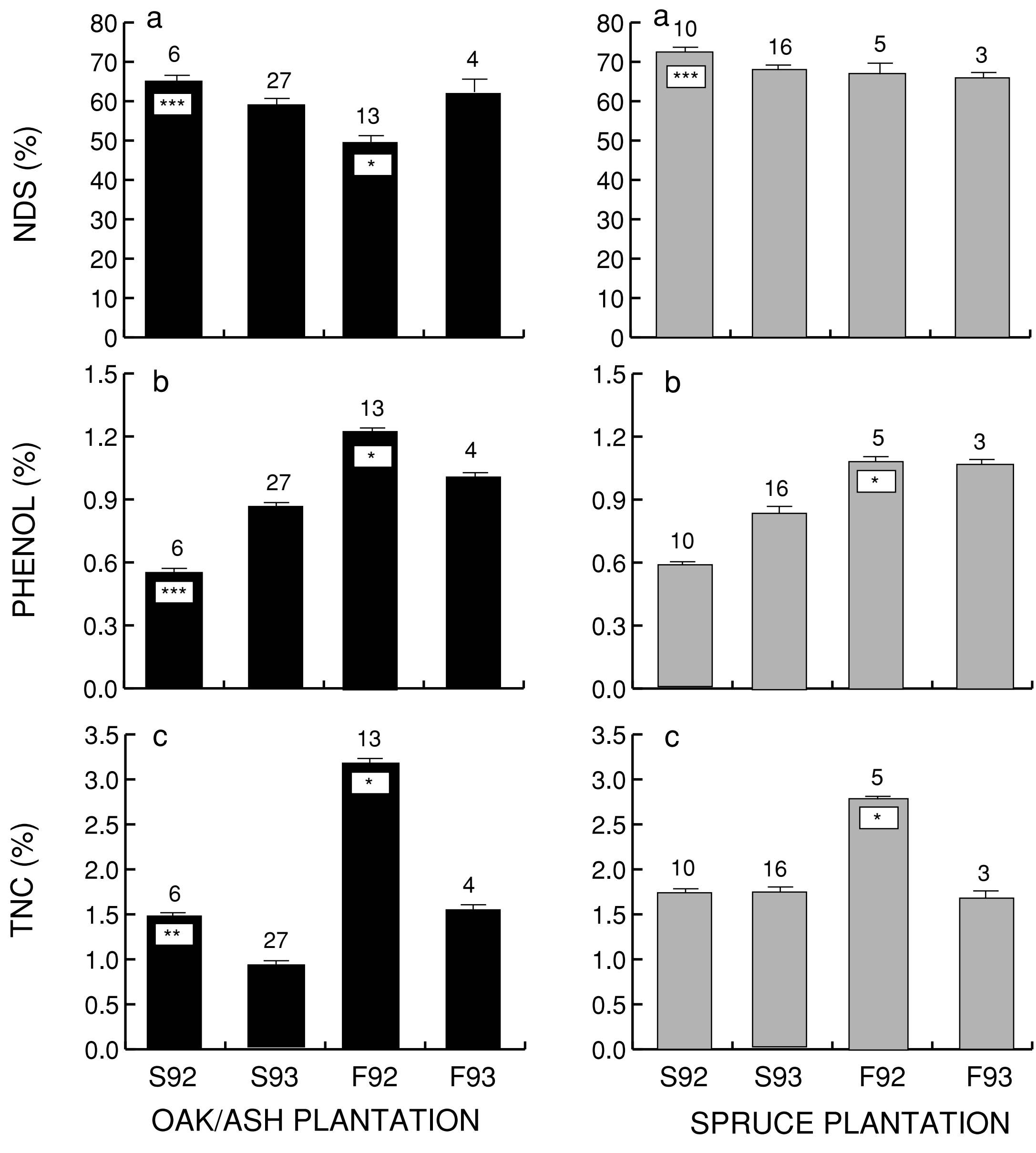

Fig. 3. Seasonal comparisons of chemical constituents of fecal matter for both types of plantation in 1992 and 1993 (*N* above *S.E.* bars). — a: neutral detergent solubles, NDS. — b: phenols. — c: total nonstructural carbohydrates, TNC. Spring (S) and Fall (F). ***$P < 0.0001$; **$P < 0.01$; *$P < 0.05$, Mann-Whitney tests for paired data.

of important cover and a decrease in food supply (Birney *et al.* 1976). Chemical analyses of vole feces collected in the old-field meadow suggested that voles used the same feeding strategies in this type of habitat, so that most of the output parameters varied similarly between both types of communities. In both habitats, there was a parallel increase in total phenolics and carbohydrates in vole feces when NDS contents decreased. We need more information on the dynamics of nutritional constraints such as fibers and phenolics, and nutrients such as carbohydrates, between the input and output digestion processes in meadow voles. Since trees in this study showed evidence of extensive bark use in both plots (Table 1 and Appendix), concurrent increases of fibers and phenolics in vole feces could be expected, but not of carbohydrates. Similar results were seen by Bergeron and Jodoin (1995) in fenced voles using bark of wild shrubs during winter. It may be that a high fiber and phenolic diet increases the passage rate of food through the gut so that more phenolics and carbohydrates remain in the fecal matter without having been processed.

I have gathered evidence, in this study, that extensive bark use by meadow voles occurred on deciduous seedlings and on wild shrubs during peak population densities. I identified a significant increase in phenolics and carbohydrates in fecal matter collected in the fall following the high summer vole densities. This needs further testing in more field situations if we want to use vole feces to predict food switches towards bark of valuable trees before bark losses occur. I was unable in this study to use chemical analyses of vole feces to discriminate between voles' bark damage on valuable trees or on wild shrubs with no commercial value. Further studies are needed if we want to manage vole populations in the more valuable tree plantations before they inflict economic losses.

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Appendix

Bark use indices (number of stems) registered on spruce trees and wild shrub species in an 8-year old Norway spruce plantation.

Square no.	*Picea abies*		*Prunus virginiana*				*Malus pumila*				*Spirea tomentosa*				*Prunus serotina*		*Cornus alternifolia*		*Spirea latifolia*				*Crataegus* sp.		
	0	1[a]	0	1	2	3	0	1	2	3	0	1	2	3	0	1	0	1	0	1	2	4	0	1	2
52	8	1	5	2			1		2	1	10	1													
58	5										0				7	3									
60	4										75							1	50						
92	8																								
125	10		12	1	2		5	1			20												2		
143	9										0	2	1												
147	5																		50		3	1	2	1	1
159	7										30														
171	6		30	6	1						20														
189	6							1			1	2							20						
198	4							1			5				4				40	1					
202	5										30						2		75						
219	4																		15	1	1				
233	6																		0						
235	2																			1	1				
261	4													1					35	1	1				
290	6					1													12						
298	5										15	2			2				0						
302	5				1	1			2		10				1				15						
351	4		1								70				2				55	2					

[a] bark use indices after Hansson (1985): — 0: no damage to stems, — 1: less than 25% of stem circumference girdled, — 2: between 25 and 50% girdled, — 3: between 50 and 75%, — 4: between 75 and 100%.