

Effects of individual bunchgrasses on potential C and N mineralization of longleaf pine savanna soils¹

J. B. West^{2,3} and L. A. Donovan

Department of Plant Biology, University of Georgia, Athens, GA 30602

WEST, J. B. AND L. A. DONOVAN. (Department of Plant Biology, University of Georgia, Athens, GA 30602). Effects of individual bunchgrasses on potential C and N mineralization of longleaf pine savanna soils.³ J. Torrey Bot. Soc. 131:120–125. 2004.—A recent conceptual model of grasslands in the US argues that, because of the discontinuous cover of plants in systems strongly limited by precipitation, the presence or absence of individual plants has significant effects on soil processes, with relatively small effects of species differences. In systems not strongly limited by precipitation, resource limitations are thought to vary in space and time, vegetation is more continuous, and species differences are relatively more important. We ask whether the model can be applied to grass species effects on potential net C and N mineralization in a southeastern US savanna ecosystem. These savannas have very sandy soils, strong soil resource limitations, and discontinuous plant cover, even though they receive 1200 mm yr⁻¹ rainfall. Based on the discontinuous herbaceous vegetation, an extension of the model would predict that native perennial bunchgrasses would have strong plant presence effects, and small or no species identity effects on these soil processes. Soils were sampled in a paired fashion, directly under a plant (either *Aristida stricta*, *Schizachyrium scoparium*, or *Andropogon ternarius*) and in adjacent unvegetated locations, and aboveground biomass was collected. Net C-min was significantly higher under plants compared to unvegetated locations, but there were also significant species identity effects, with the greatest rates observed under *A. stricta*. This pattern is likely explained by the greater biomass of *A. stricta*, because net C-min was positively related to biomass. For net N-min, there were neither plant presence nor species identity effects. There was, however, a positive relationship between net C-min and net N-min for both *S. scoparium* and *A. ternarius* soils, but not for *A. stricta*, suggesting a subtle, but potentially important, difference among species in their effects on N cycling. The results suggest that individual grasses have significant effects on soil processes in this system, but that the conceptual model developed for grasslands may not generalize to the effects of grasses on the soils of these savannas.

Key words: bluestem, carbon, mineralization, nitrogen, savanna, wiregrass.

Individual plants play critical roles in terrestrial ecosystem function, especially with respect to their effects on soil element cycling and soil organic matter dynamics. A recent conceptual model of plant-soil interactions in temperate grasslands (Burke et al. 1998, see also Vinton and Burke 1995, 1997) makes predictions about the influences of individual plants on their soil environment across a large gradient in annual rainfall. They argue that rainfall primarily limits plant growth in low rainfall zones, and refer to these systems as “belowground dominance” systems. Whereas with increasing precipitation, plants become relatively more limited by the availability of other resources such as light or nitrogen, or by the actions of herbivores or fire

and are referred to as “indeterminate dominance” systems to reflect the temporal and spatial variability of resources. Above some precipitation threshold, plants become primarily limited by light in “aboveground dominance” systems in this model (Burke et al. 1998). In “belowground dominance” systems plant cover is discontinuous and the effect of the presence of individual plants on soil processes is large relative to areas unoccupied by plants. These individual plants may produce resource islands that have been well described in semi-arid systems, and are primarily the result of continual litterfall of stationary plants (Hook et al. 1991, Reynolds et al. 1999, Derner and Briske 2001). The differences among species in traits such as tissue chemistry or lifespan, however, are predicted to have a relatively small effect on soil processes in these systems. As systems become less limited by precipitation, plant cover becomes more continuous and the differences among species in litter chemistry, phenology, and tissue lifespan become more important than the presence or absence of individual plants (Wedin and Tilman 1990, Epstein et al. 1998, Van der Krift and Berendse 2001). This model is based primarily on research in the semi-arid

¹ Funding from the National Science Foundation (DEB00-72943) and the Andrew W. Mellon Foundation supported this work.

² We thank the staff at CSNWR for housing on site and permission to conduct this research and Jill Johnston for help with fieldwork. The manuscript was improved by comments from two anonymous reviewers.

³ Current address: Department of Ecology, Evolution and Behavior, University of Minnesota, St. Paul, MN 55114.

Received for publication July 16, 2003, and in revised form November 12, 2003.

to sub-humid grasslands of North America, although the authors suggest that it may apply to grasslands worldwide. Our understanding of grassland ecosystem function would improve considerably if this model could be extended to other grasslands and grass-dominated systems such as savannas.

We report here a study of the effects of dominant, C₄ perennial bunchgrasses on soil microbial respiration (potential net C mineralization: net C-min) and inorganic N production (potential net N mineralization: net N-min) in laboratory incubations of field-collected soils. *Aristida stricta* Michx. (wiregrass), *Schizachyrium scoparium* (Michx.) Nash (little bluestem), and *Andropogon ternarius* Michx. (splitbeard bluestem) are C₄ perennial bunchgrasses native to *Pinus palustris* Miller (longleaf pine) savannas. These savannas are characterized by a very open overstory of longleaf pine trees and subordinate oaks (*Quercus* spp.), and an herbaceous layer dominated by these grasses. Physiological, distributional and successional differences between the study species suggest that *A. stricta* is more stress-tolerant (*sensu* Grime 2001) than the bluestems (West 2002, West et al. 2003). *Aristida stricta* dominance tends to increase on the most nutrient-poor, xeric sites of the sandhills where the bluestems are rarely found, although these species often co-occur on sites with intermediate soil resource availability where this study was conducted. *Aristida stricta* does not readily colonize after a soil disturbance, whereas the bluestems often do so (Lemon, 1949, Grelen, 1962). *Aristida stricta* has green leaves year-round, whereas the bluestems are winter deciduous, and, consistent with a nutrient retention strategy (Aerts and Chapin 2000), the roots of *A. stricta* exhibit considerably higher lifespans than those of *S. scoparium* (West et al. 2003). Finally, comparisons of leaf tissue C:N ratios from several sites revealed consistently higher C:N ratios in all tissues for *A. stricta* (leaf C:N = 98.64) relative to the bluestems (*S. scoparium* = 44.54, *A. ternarius* = 41.24; West 2002). Trait differences such as these have been found to result in significant species identity effects on soil processes in other species (e.g., Wedin and Tilman 1990, Epstein et al. 1998, Van der Krift and Berendse 2001).

Mean annual precipitation at our site is 1200mm, placing these savannas towards the high end of the precipitation gradient described by Burke et al. (1998). However, the soils are very sandy (> 90% sand), and show strong soil

resource limitation (Christensen 1988, Wilson et al. 1999, West 2002). In addition, consistent with significant soil resource limitation, plant cover on the intermediate to sandiest sites is often discontinuous (West, pers. obs.). As a result, although precipitation is relatively high, based on the discontinuous nature of the vegetation, we believe that this savanna ecosystem is most appropriately classified as a belowground-dominance system (Burke et al. 1998). Therefore, we predicted that (1) plant presence would significantly increase net C-min and net N-min relative to unvegetated locations, and (2) in spite of known trait differences among the study species, species identity would not significantly affect net C-min or net N-min.

Materials and Methods. The fieldwork for this study was conducted at the Carolina Sandhills National Wildlife Refuge (CSNWR, near McBee, South Carolina, USA). This site selected for sampling was burned in spring 2000 and has received frequent prescribed burns (approximately 5-yr return interval) for 20 years. It was dominated by a relatively sparse overstory of *P. palustris* and a mixture of *Quercus* species. In April 2001, 20 blocks were located along an approximately 100 m transect within the Alpin (Typic Quartzipsamment) soil series on the site. The soils contain > 90% sand and are very N poor (West 2002). Each block contained one individual of each species (*A. stricta*, *S. scoparium*, and *A. ternarius*) located less than 1.5 m from each other. The aboveground biomass of each entire tuft was clipped and placed in paper bags. Soil was sampled from the mineral soil surface to a depth of 10 cm (5.5 cm diameter core) in a paired design. A core was taken from the center of each plant and another from an unvegetated location (15 cm away from the edge of the target plant and at least 10 cm from any other stem). Contrary to what is observed for arid and semi-arid grasslands (Burke et al. 1999), no raised hummocks are evident in our system, so the surface of the soil "under" plants is at the same elevation as those in the "open". Each core was quickly placed in a plastic bag and then stored in a cooler with ice until all of the cores were moved to a 3° C cold room (less than 8 hr later).

Laboratory incubations were conducted to determine potential net C mineralization and net N mineralization rates for the sampled soils (Hart et al. 1994b). The bagged, moist soil samples were sieved (2mm diameter mesh) to remove

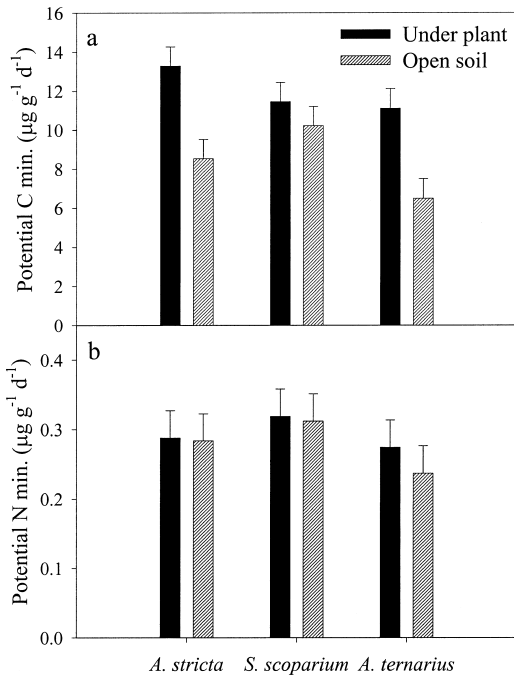


Fig. 1. Mean potential net C mineralization (a) and N mineralization (b, + 1 SE) for locations under individual plants and paired unvegetated locations for each species. There was a significant effect of plant presence ($P < 0.02$) and species identity ($P < 0.0001$) on potential C mineralization, and a significant interaction of plant presence and species identity ($P < 0.05$). There were no significant effects of plant presence or identity on N mineralization (see Table 1 for results of the statistical analysis).

large roots and litter prior to extraction. Four-gram subsamples were placed in flasks with 20 ml of 2 M KCl. These were shaken for 1 hour, then the solutions were centrifuged and the clear supernatant was pipetted into vials. The vials were stored at 3°C until analysis by continuous flow colorimetry (Alpkem RFA300, OI Corp., College Station, TX). Soil incubations (20g soil wet wt.) were conducted in glass incubation chambers. The chambers consisted of 400 ml Mason jars that included a vial with 4 ml of 1.5 M NaOH to serve as a CO_2 trap (Zibilske 1994). To ensure the atmosphere in the chamber remained water saturated, 10 ml of distilled water was added to the bottom of the jars. "Blank" chambers were also set up and incubated without soil for baseline CO_2 determination. All chambers were closed tightly and incubated in the dark at 23°C for 31 days.

Following the incubation, a 4 g soil subsample was extracted and analyzed as before. A second subsample was used to determine gravimet-

Table 1. Results of mixed-model ANOVAs for potential net C and N mineralization. The effects of species identity, location (paired samples: under a plant versus open soil), and the interactions were tested.

Source	nDF	dDF	F	P
C mineralization				
Species	2	87	4.77	0.01
Location	1	87	28.83	<0.0001
Species * Location	2	87	3.03	0.05
N mineralization				
Species	2	90	0.44	0.64
Location	1	90	1.56	0.22
Species * Location	2	90	0.01	0.99

ric moisture content. Potential net N-min was calculated as the amount of inorganic N accumulated during the incubation (Hart et al. 1994b). Potential net C-min was calculated from titration of the NaOH traps with standardized 1% HCl. The quantity of CO_2 evolved was calculated as the difference between the mean normality of the "blank" traps and the normality of the sample traps (Zibilske 1994). Rates are expressed on a dry soil weight basis per day.

Mixed-model ANOVAs (block as a random effect, and plant presence: under plant / unvegetated, and species identity: *A. stricta* / *A. ternarius* / *S. scoparium* as fixed effects; Littell et al. 1996) were carried out to determine the effects of plant presence and species identity on net C-min and net N-min. For all ANOVA-based analyses data were transformed as necessary to satisfy model assumptions. Correlation analyses were also conducted to determine the relationships between plant biomass and net C-min and net N-min, and the relationships between net C-min and net N-min for each species.

Results. Net C-min was greater for soils collected directly under individual plants as compared to the paired, unvegetated locations (Figure 1a). This effect of plant presence on net C-min, however, differed among species, with the highest rate found under *A. stricta* plants (Table 1). This difference among species is partially explained by the significant, positive relationship found between aboveground plant biomass and net C-min (Figure 2). Aboveground biomass was significantly greater for *A. stricta* (mean = 30.71 g, 1 S.E. = 3.06) than for the other two species (*A. ternarius* = 12.77 g \pm 3.06, *S. scoparium* = 12.05 g \pm 3.06, $F_{2,38} = 16.27$, $P < 0.0001$), consistent with the higher rates of net C-min observed in the soils from *A. stricta*.

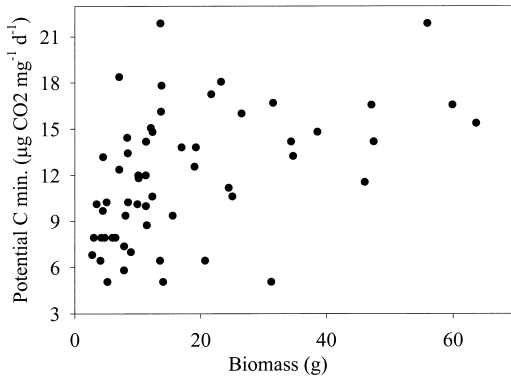


Fig. 2. The relationship between biomass and potential net C mineralization ($P < 0.01$, Spearman correlation coefficient = 0.51).

Contrary to the results for net C-min, however, there was no significant effect of plant presence or species identity on net N-min (Figure 1b) and no relationship was found between biomass and net N-min (data not presented).

The relationship between net C-min and net N-min differed between species (Figure 3). There was a positive relationship between net C-min and net N-min for *S. scoparium* and *A. ternarius*, showing greater net inorganic N production with increased microbial respiration. There was also a positive relationship between net C-min and net N-min for unvegetated locations ($P < 0.01$, data not presented). However, no significant relationship between net C-min and net N-min was found for *A. stricta* ($P = 0.60$).

Discussion. Consistent with our predictions, the presence of individual plants significantly stimulated the microbial activity of soils in which they were growing. Soils collected under individual plants showed greater net C-min than did soil collected 15 cm away from the edge of the plant canopy, consistent with the effect of litter input from root and leaf turnover of individual plants. However, in disagreement with our predictions, there were also significant differences among species in their effects on net C-min. The positive correlation between above-ground plant biomass and net C-min suggests that larger plants supply greater amounts of litter to soils, thus increasing microbial activity (Robles and Burke 1997). Although we specifically attempted to choose a site where plants were of similar sizes, *A. stricta* plants were significantly larger than either of the other two species, and this likely explains the significant species effect we found. The greater size of *A. stricta* is con-

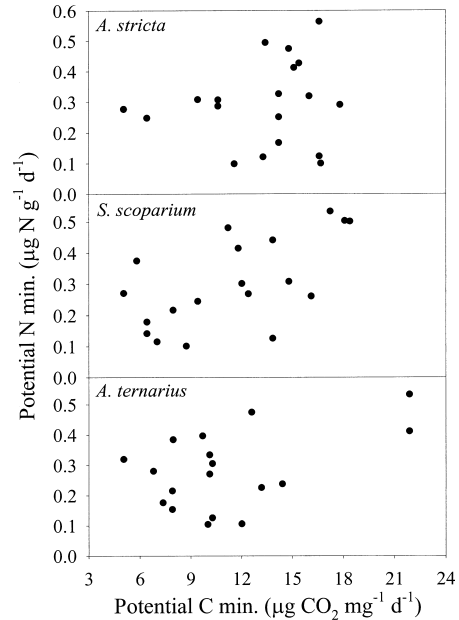


Fig. 3. Relationships between potential net C mineralization and net N-mineralization for *A. stricta* ($P = 0.60$), *S. scoparium* ($P < 0.01$, Spearman correlation coefficient = 0.61), and *A. ternarius* ($P = 0.05$, Spearman correlation coefficient = 0.46).

sistent with previous arguments of greater nitrogen use efficiency in this species (Chapin 1980, West et al. 2003). Higher nitrogen use efficiency, as indicated by higher tissue C:N ratios and long root lifespans, as well as winter photosynthesis supporting winter shoot and root growth (West et al. 2003), may provide a long-term growth advantage to *A. stricta* in this nutrient-limited system (Aerts and Chapin 2000). Although we cannot rule out such effects as small-scale disturbances and differential colonization ability among these species (Grelen 1962), our results suggest that species differences in resource use efficiency may have significant consequences for soil microbial activity in this system.

This clear influence of plant presence and species identity on microbial respiration, however, did not result in any direct effect of these grasses on net N-min. These results are consistent with a previous sampling of two additional sites (both also with discontinuous plant cover and similar soil types) that showed no significant effect of these species on net N-min (West 2002). Given the observed increase in net C-min due to plant inputs and the species-specific nature of that effect, what explains the absence of a species-specific effect on net N-min? The relationships between net N-min and net C-min for soils col-

lected under *A. ternarius* and *S. scoparium* showed positive relationships between microbial respiration and net production of inorganic N (as was also the case in unvegetated soils, data not presented). This would be expected if the microbial communities are more limited by carbon than nitrogen in those soils (Cheng et al. 1996) and if, as has been suggested (Hart et al. 1994a), increased microbial respiration indicates increased gross N mineralization. In *A. stricta* soils, however, there was no such relationship, although a wide range of net C-min was observed. This may indicate greater microbial N-limitation in *A. stricta* soils, which would be consistent with the greater C:N ratios of the litter input of this species.

Our results suggest that individual plant influences on soil processes in this system are not well predicted by the Burke et al. (1998) model, and further that these influences may be process-specific. Some caveats are required in interpreting our results. First, further research that explicitly included variation across sites would significantly improve our ability to generalize about these savannas. In addition, our results represent potential mineralization rates. Microbial activity in the field is subject to changes in moisture and temperature and other factors that can significantly affect these processes. Finally, we know that the influences of trees on soil processes are important in this system (Espeleta 2002). However, it is not known how these influences interact with the effects of grasses. In addition, since these are fire-maintained systems, fire, plants, and soil resources likely interact and these interactions are even less well understood. As has been argued previously, savannas may represent a unique biome where predictions developed for grasslands or forests may not directly apply (Scholes and Archer 1997, Reich et al. 2001), and more research into the dynamics of these interesting biomes is clearly needed.

Conclusions. Individual, dominant bunchgrasses influenced soil microbial activity in this system. We found partial support for the conceptual model of Burke et al (1998), but no consistency in the effects on the two soil processes observed. For net C-min this was likely due to the species-specific differences in plant size we observed. The relatively larger individuals of *A. stricta* caused increased rates of microbial activity in the soils they occupied. We observed no direct effects of individual plants on net N-min suggesting that factors other than the presence

or absence of individual grasses may be more important for net N-min in this system. We found support for differences among species in how they affect the relationship between C and N mineralization. As has been suggested before (Hart et al. 1994a), more detailed analyses of the linkages between C and N cycling and how plants affect those processes would considerably improve our understanding of plant-soil interactions.

Literature Cited

- AERTS, R., AND F. S. CHAPIN 2000. The mineral nutrition of wild plants revisited: A re-evaluation of processes and patterns. *Adv. Ecol. Res.* 30: 1–67.
- BURKE, I. C., W. K. LAUENROTH, R. RIGGLE, P. BRANNEN, B. MADIGAN, AND S. BEARD. 1999. Spatial variability of soil properties in the shortgrass steppe: The relative importance of topography, grazing, microsite, and plant species in controlling spatial patterns. *Ecosystems* 2: 422–438.
- BURKE, I. C., W. K. LAUENROTH, M. A. VINTON, P. B. HOOK, R. H. KELLY, H. E. EPSTEIN, M. R. AGUIAR, M. D. ROBLES, M. O. AGUILERA, K. L. MURPHY, AND R. A. GILL. 1998. Plant-soil interactions in temperate grasslands. *Biogeochem.* 42: 121–143.
- CHAPIN, F. S. 1980. The mineral nutrition of wild plants. *Ann. Rev. Ecol. Syst.* 11: 233–260.
- CHENG, W. X., Q. L. ZHANG, D. C. COLEMAN, C. R. CARROLL, AND C. A. HOFFMAN. 1996. Is available carbon limiting microbial respiration in the rhizosphere? *Soil Biol. & Biochem.* 28: 1283–1288.
- CHRISTENSEN, N. L. 1988. Vegetation of the southeastern coastal plain. p. 317–363. *In* M.G. Barbour and W. D. Billings [eds.], *North American terrestrial vegetation*. Cambridge University Press, New York, NY.
- DERNER, J. D., AND D. D. BRISKE. 2001. Below-ground carbon and nitrogen accumulation in perennial grasses: A comparison of caespitose and rhizomatous growth forms. *Plant and Soil* 237: 117–127.
- EPSTEIN, H. E., I. C. BURKE, AND A. R. MOSIER. 1998. Plant effects on spatial and temporal patterns of nitrogen cycling in shortgrass steppe. *Ecosystems* 1: 374–385.
- ESPELETA, J. F. 2002. Species-specific patterns of fine root demography and hydraulic lift among trees of the fall-line sandhills. Ph. D. dissertation. University of Georgia, Athens, GA.
- GRELEN, H. 1962. Plant succession on cleared sandhills in northwest Florida. *Am. Midl. Nat.* 67: 36–42.
- GRIME, J. P. 2001. *Plant Strategies, Vegetation processes and ecosystem properties*. Wiley, New York, NY. 417 p.
- HART, S. C., G. E. NASON, D. D. MYROLD, AND D. A. PERRY. 1994a. Dynamics of gross nitrogen transformations in an old-growth forest—the carbon connection. *Ecology* 75: 880–891.
- HART, S. C., J. M. STARK, E. A. DAVIDSON, AND M. K. FIRESTONE. 1994b. Nitrogen mineralization, immobilization, and nitrification. p. 985–1018. *In* R.W. Weaver et al. [eds.], *Methods of soil analysis: microbial and biochemical properties, part 2*. Soil Science Society of America, Madison, WI.

- HOOK, P. B., I. C. BURKE, AND W. K. LAUENROTH. 1991. Heterogeneity of soil and plant n and c associated with individual plants and openings in North American shortgrass steppe. *Plant and Soil* 138: 247–256.
- JACKSON, R. B., J. CANADELL, J. R. EHLERINGER, H. A. MOONEY, O. E. SALA, AND E. D. SCHULZE. 1996. A global analysis of root distributions for terrestrial biomes. *Oecologia* 108: 389–411.
- LITTELL, R. C., G. A. MILLIKEN, W. W. STROUP, AND R. D. WOLFINGER RD. 1996. SAS system for mixed models. SAS Institute Inc., Cary, NC. 633 p.
- REICH, P. B., D. W. PETERSON, D. A. WEDIN, AND K. WRAGE. 2001. Fire and vegetation effects on productivity and nitrogen cycling across a forest-grassland continuum. *Ecology* 82: 1703–1719.
- REYNOLDS, J. F., R. A. VIRGINIA, P. R. KEMP, A. G. DE SOYZA, AND D. C. TREMMEL. 1999. Impact of drought on desert shrubs: Effects of seasonality and degree of resource island development. *Ecol. Monogr.* 69: 69–106.
- ROBLES, M. D., AND I. C. BURKE. 1997. Legume, grass, and conservation reserve program effects on soil organic matter recovery. *Ecol. Appl.* 7: 345–357.
- SCHOLES, R. J., AND S. R. ARCHER. 1997. Tree-grass interactions in savannas. *Annu. Rev. Ecol. Syst.* 28: 517–544.
- VAN DER KRIFT, T. A. J., AND F. BERENDSE. 2001. The effect of plant species on soil nitrogen mineralization. *J. Ecol.* 89: 555–561.
- VINTON, M. A., AND I. C. BURKE. 1995. Interactions between individual plant-species and soil nutrient status in shortgrass steppe. *Ecology* 76: 1116–1133.
- VINTON, M. A., AND I. C. BURKE. 1997. Contingent effects of plant species on soils along a regional moisture gradient in the Great Plains. *Oecologia* 110: 393–402.
- WEDIN, D. A., AND D. TILMAN. 1990. Species effects on nitrogen cycling—a test with perennial grasses. *Oecologia* 84: 433–441.
- WEST, J. B. 2002. The effects of dominant bunchgrass species on sandhill longleaf pine savanna ecosystem function: A comparison of wiregrass to the bluestems. Ph.D. thesis. University of Georgia, Athens, GA. 121 p.
- WEST, J. B., J. F. ESPELETA, AND L. A. DONOVAN. 2003. Differences in root longevity and phenology between two co-occurring, native sandhill savanna bunchgrasses. *Functional Ecology* 17: 20–28.
- WILSON, C. A., R. J. MITCHELL, J. J. HENDRICKS, AND L. R. BORING. 1999. Patterns and controls of ecosystem function in longleaf pine—wiregrass savannas. II. Nitrogen dynamics. *Can. J. For. Res.* 29: 752–760.
- ZIBILSKE, L. M. 1994. Carbon mineralization. p. 835–863. *In* R.W. Weaver et al. [eds.], *Methods of soil analysis: microbial and biochemical properties*, part 2. Soil Science Society of America, Madison, WI.