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COMPARISON OF SOIL CORING AND INGROWTH METHODS FOR MEASURING BELOWGROUND PRODUCTION

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Measurement of belowground primary production in grasslands and marshes has been a particularly troubling problem, but is crucial to understanding a variety of ecosystem properties because a sizable proportion of total biomass and production occurs belowground. Most estimates of seasonal changes in belowground biomass have been obtained by harvesting soil cores and separating live and dead material (Böhm 1979). Production is typically calculated from soil core data as maximum minus minimum biomass or as some function of seasonal incremental differences in biomass, dead organic material, or both.

Conceptually most authors agree that calculations based on soil cores underestimate net production because: (1) seasonal maxima and minima do not exactly coincide with sampling dates, (2) losses occur due to grazing, sloughing, and exudation, and (3) growth and mortality occur simultaneously during a sampling interval. However, some authors (Persson 1978, Singh et al. 1984, Sala et al. 1988) have shown that sampling variability and bias caused by selection of only nonzero positive increments lead the most commonly used techniques to overestimate net production. Overestimation error is larger when biomass is sampled over more frequent intervals or when more components (dead, live, recent dead, etc.) are included. Some error caused by sampling variability can be reduced by including in the calculations of net production only intervals in which biomass at the beginning and end of the interval were significantly different. Such constraints reduce but do not eliminate the overestimation problem (Singh et al. 1984).

Techniques that measure root ingrowth into root-free soil enclosed in mesh bags (Lund et al. 1970, Persson 1983, Steen 1985) provide an alternative to soil cores. Ingrowth methods avoid the high labor and high variability associated with sorting live and dead roots from native soil and allow clear identification of the time period in which root growth occurred, but they do not eliminate the problem of simultaneous biomass production and loss, and may create additional problems of disturbance associated with coring or differences in soil conditions (e.g., root densities, nutrient concentrations, penetration resistance) inside the bags.

This paper evaluates soil cores and a mesh bag method for measuring net belowground production in a prairie marsh in Manitoba, Canada.

Methods

Data were collected from May 1989 to April 1990 from a seasonally flooded stand of whitetop grass (*Scolochloa festucacea* [Willd.] Link) in the Delta Marsh, a 20 000-ha lacustrine prairie marsh at Delta, Manitoba, Canada (50°11′ N, 98°19′ W). The study site was a 25-ha impoundment with whitetop cover >99%. Soils (0–15 cm depth) were of loam texture and had 20% organic matter, a bulk density of 1.35 g/cm^3, pH of 7.0, and electrical conductivity of 10–20 mS/cm.

Belowground biomass was sampled to a depth of 25 cm using a 15 cm diameter metal corer. Six replicate cores were collected monthly from May to August 1989 and once in April 1990 from two locations ≈200 m apart in the impoundment. Each sampling date, a point in each area was selected at random and cores collected every 3 m along a line from that point. Samples were never taken within 5 m of previous core hole locations. Cores were washed through a screen (1.5 mm mesh) and sorted into live rhizomes, live roots, and necromass (dead roots and unidentifiable organic matter) based on color and consistency. Sorted material was rewashed with tap water, dried at 50°C, and weighed. Ash content was determined for a subset of roots and rhizomes and averaged between 6.6 and 8.0% of dry mass. Ash did not differ among roots and rhizomes or among sampling dates. Biomass values are reported as dry mass.

Belowground net primary production (NPP) was calculated from the soil core data according to several different algorithms (see Table 1). Where possible, all the calculations of NPP using differences in biomass or necromass were performed with and without testing for significant differences. Significance was based on pairwise t tests (Fisher's LSD), with $P < .05$.

Mesh bags for root and rhizome ingrowth measurement were made from fiberglass window screen (1.5 mm mesh) and measured 30 cm long and 6.0 cm diameter. They were open at the top and sewn closed at the bottom. Bags were filled with a sandy soil from the Delta Marsh that was sieved free of particulate organic matter. This soil was sandier (91 vs. 50% sand), lower in organic matter (9 vs. 20%) and extractable inorganic nitrogen (1–3 vs. 3–10 μg/g dry soil), but greater in bulk density (1.70 vs. 1.35 g/cm^3) compared with marsh

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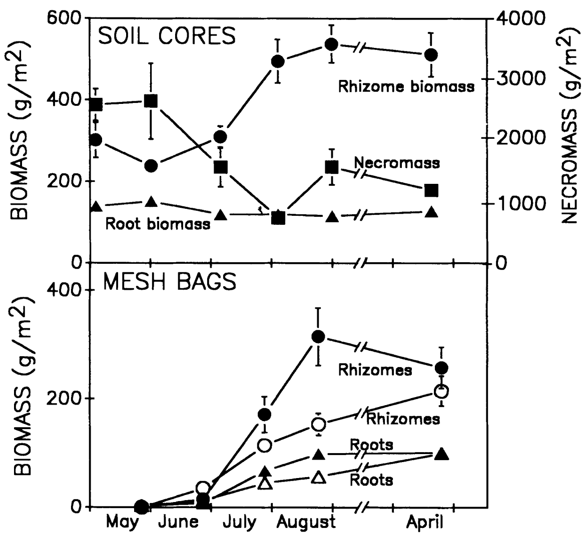

FIG. 1. Seasonal patterns of root and rhizome dry biomass and necromass from soil cores (top) and mesh bags (bottom). For mesh bags, solid symbols represent ingrowth into long-term bags, open symbols represent cumulative ingrowth into short-term bags. All error bars are ± 1 SE. Sample sizes are $n = 6$ for soil cores, $n = 8$ for mesh bags.

soil. Bags were deployed in rows 5 m apart, with 8 bags/row and 2 m between bags. Bags were installed by removing a 6 cm diameter core with a core tube and inserting the bag to a depth of 25 cm. Bags were retrieved by slicing the soil at a distance of ≈ 2 cm from the bag with a knife, removing the bag plus attached soil from the ground and carefully cutting away excess soil and roots and rhizomes that had penetrated the bag. Although the mesh size of the bags was smaller than the average diameter of whitetop rhizomes (2–4 mm), rhizome tips easily penetrated and grew into the bag. After retrieval, bag contents were washed free of sediment, separated into roots and rhizomes, dried, and weighed.

Long- and short-term mesh bags were deployed with overlapping time periods to allow calculation of biomass losses between sampling intervals (Steen 1985). In April 1989, 40 long-term bags were set out at the same two locations where biomass cores were taken. Eight replicate bags were then collected at roughly monthly intervals from May to late August 1989 and again in April 1990. In addition, eight short-term bags were set out at each location each month and collected at the next sampling date. Thus, all of the short-term bags were deployed for ≈ 1 mo, except for the bags set out in late August, which were collected the following April.

Turnover losses were calculated as the differences in biomass between the sum of the short-term bags and the long-term bags for each interval, when the sum of the biomass in the short-term bags was greater than the corresponding long-term bags. NPP was estimated from the mesh bags in the following ways: (1) the sum of the biomass increments in the short-term bags, (2) the total biomass accumulation in the set of long-term bags left out for 1 yr, (3) the sum of the peak root and peak rhizome biomass in the long-term bags, and (4) the total biomass accumulation in the 1-yr long-term bags plus turnover losses. Standard errors of estimates

TABLE 1. Belowground net annual primary production (NPP) and formulas used to calculate production from soil cores. Significant differences were based on Fisher's least significant difference test (LSD), $P < .05$. Symbols are: LT = live total biomass (rhizomes + roots); LRh = live rhizomes; LR = live roots; NT = necromass.

	Belowground NPP (g/m², $\bar{X} \pm 1$ SE)			
	All increments	Significant differences only	Method	Source*
Maximum − minimum biomass	263 ± 63	263 ± 63	$LT_{max} - LT_{min}$	1
Maximum − minimum biomass	312 ± 58	300 ± 52	$(LRh_{max} - LRh_{min}) + (LR_{max} - LR_{min})$	2
Biomass increments only	263 ± 124	186 ± 75	$\Sigma\ \Delta LT,\ \Delta LT > 0$	3
Biomass increments only	324 ± 107	186 ± 60	$\Sigma(\Delta LRh + \Delta LR),\ \Delta LRh > 0,\ \Delta LR > 0$	4
Necromass increments only	902 ± 736	0	$\Sigma\ \Delta NT,\ \Delta NT > 0$	5
Biomass + necromass increments	1115 ± 749	186 ± 75	Smalley method	6
Biomass + necromass increments	891 ± 731	0	$\Sigma(\Delta LT + \Delta NT),\ \Delta LT > 0,\ \Delta NT > 0$	7

* Sources for methods: (1) Dahlman and Kucera 1965; (2) as method 1, differences for roots and rhizomes calculated separately; (3) Singh and Yadava 1974; (4) as method 3, root and rhizome increments summed separately; (5, 7) Hansson and Steen 1984; (6) Smalley 1958.

TABLE 2. Net annual belowground primary production (g/m², mean ± 1 SE) calculated from mesh bag technique.

	Roots	Rhizomes	Total
Sum of short-term bags	100 ± 7	215 ± 27	315 ± 31
Last long-term bags	101 ± 11	258 ± 38	359 ± 44
Peak in long-term bags	101 ± 11	315 ± 53	416 ± 54
Last long-term bags + turnover	147 ± 19	396 ± 78	543 ± 81

of biomass losses and NPP from both soil cores and mesh bags were calculated from pooled variances. The variances of the differences between two sampling times were calculated as described by Hansson and Steen (1984).

Results

Soil cores showed that rhizome biomass reached a seasonal minimum in early June and a maximum in late August, root biomass remained relatively constant during the year, and necromass was greater than total biomass except in early August when they were approximately equal (Fig. 1, top). Root and rhizome ingrowth to the mesh bags was small during May and June and great during midsummer (Fig. 1, bottom). During the period of greatest rhizome ingrowth, the long-term bags measured greater biomass than the sum of the short-term bags for the same interval (Fig. 1, bottom). Seasonal patterns between long- and short-term bags were similar in spring and summer, but between September and April biomass in the long-term bags decreased while it continued to increase in the short-term bags (Fig. 1). The majority of root ingrowth occurred during July and August, and root ingrowth was very similar between long- and short-term bags (Fig. 1, bottom).

Calculations of NPP from the soil cores based on seasonal maxima and minima and summed biomass increments gave similar estimates of 263–324 g/m² (Table 1). Calculations in which roots and rhizomes were summed separately (methods from references 2 and 4) yielded higher NPP than methods based on aggregated root plus rhizome biomass (methods 1 and 3). Including differences only when they were statistically significant lowered some estimates (methods 2–4), but had no effect using the overall maximum minus minimum (method 1) because the difference between the overall maximum and minimum was significant (Table 1). Including necromass in the calculation of NPP (methods 5–7) produced estimates that were highly variable and up to 3 times greater than the estimates derived from increments of biomass only (Table 1).

Estimates of annual NPP from the mesh bags (315–543 g/m²) were similar or greater than estimates from soil cores. Ingrowth into long-term bags yielded higher values than the sum of the short-term bags (Table 2). Peak biomass of roots plus rhizomes in the long-term bags provided a higher estimate than the biomass in the last (April 1990) set of long-term bags because root and rhizome peaks occurred at different times. Losses from the mesh bags were low or zero during spring and summer and high between September and April. Between September and April rhizome biomass declined in the long-term bags but increased in the short-term bags. This indicated that older roots and rhizomes in the long-term bags were lost, but growth of new roots and rhizomes continued during the interval. Adding this estimate of losses to the total live biomass in the last long-term bags yielded the highest estimate of 543 g/m² (Table 1).

Discussion

Both soil coring and mesh bag ingrowth techniques have practical and theoretical limitations yet yielded reasonably similar estimates of annual belowground NPP when compared directly in the same ecosystem. The mesh bag method produced higher estimates than soil coring techniques of maximum − minimum biomass or sequential sums of biomass increment calculations. Separating out changes in root and rhizome biomass increased NPP estimated from soil cores but not unreasonably. Conceptually, sequential biomass increment methods that select significant differences only may be superior to maximum − minimum and biomass increment calculations based on all differences, but in practice all produced estimates within the range of sampling error. Methods that included necromass gave a wide range of estimates, some of which were greatly inflated compared with the mesh bags and soil coring methods that used biomass only. Necromass was variable and greater than biomass, so errors in this compartment overwhelmed and masked any real changes that could be measured in biomass.

Consistently higher biomass measured in the long-term mesh bags compared with the sum of the short-term bags indicated a disturbance effect associated with insertion of the mesh bags. This disturbance would cause short-term bags to underestimate NPP severely while causing lower but potentially important underestimation by the long-term bags. The estimate of annual NPP obtained from the peak biomass in the 1-yr set of long-term mesh bags (416 ± 54 g/m²) could therefore be considered to be biased downward. The estimate of NPP from peak or year-long deployment of mesh bags also did not take into account any annual losses. Including estimates of monthly losses raised the estimate to 543 ± 81 g/m², but because losses were calculated from incremental differences selected only when they were positive, a portion of the annual loss may be attributable solely to sampling error.

It is also possible that root and rhizome growth into the mesh bags was higher than in undisturbed soil because the bags provided soil uncolonized by other roots. This was unlikely because soil in the bags was roughly equivalent or poorer in nutrients than unaltered soil from the study site. Root and rhizome ingrowth could have been enhanced by reduced resistance to penetration or reduced competition. The importance of these factors was not determined.

The total accumulation of roots and rhizomes in the long-term mesh bags approached but did not equal the total biomass in the soil cores. Root and rhizome biomass, respectively, reached 101 and 315 g/m² in the mesh bags and 150 and 525 g/m² in the cores. This suggests that some roots and rhizomes may live longer than 1 yr and that the biomass of roots and rhizomes measured in the cores represents tissues produced during more than 1 yr. Comparison of long- and short-term mesh bags also showed that a substantial loss of roots and rhizomes occurred between September and April. Losses represented 37% of peak late-summer rhizome biomass and 40% of peak root biomass.

The soil coring techniques that gave the most reasonable and consistent results (maximum − minimum and sequential biomass increments) were also the simplest. This supports the general conclusion that measuring fewer parameters provides a more accurate measure of NPP. Coring twice a year and sorting live roots and rhizomes would appear to provide a reasonable estimate of NPP in this ecosystem. Mesh bags offer a more efficient technique for quantifying belowground production once relationships to soil coring methods are known. Simple 1-yr deployments of long-term bags or long-term bags coupled with nongrowing-season deployment of short-term bags would provide reasonable estimates of NPP, especially if disturbance effects could be minimized by setting bags out in early spring or early fall, when data from soil cores indicate rhizome growth is low. These simple mesh bag methods would reduce the labor involved in estimating belowground NPP and give estimates reasonably close to those based on soil cores.

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