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CARBON DYNAMICS AND ESTIMATES OF PRIMARY PRODUCTION BY HARVEST, ^{14}C DILUTION, AND ^{14}C TURNOVER[1]

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Abstract. Large plots of native shortgrass steppe were labeled with ^{14}C to assess short-term patterns of carbon allocation and the long-term process of herbivory, death, and decomposition, and to compare estimates of net aboveground, crown, and root primary production using ^{14}C dilution, ^{14}C turnover, and traditional harvest methods.

Stabilization of labile ^{14}C via translocation, incorporation into structural tissue, and respiration and exudation required one growing season. Exudation was 17% of plant ^{14}C after stabilization. Estimates of turnover time for leaves, crowns, and roots by ^{14}C turnover were 3, 5, and 8 yr, respectively, yielding estimates of belowground production that were much lower than previously thought. Estimates of aboveground production by ^{14}C turnover were close to those obtained by harvest of peak-standing crop, but lower than reported values obtained by harvest maxima-minima. Estimates of root production by harvest maxima-minima were zero in 2 of 4 yr. ^{14}C turnover appeared to provide reliable estimates of aboveground, crown, and root production. In contrast to reliable estimates by ^{14}C turnover, ^{14}C dilution estimates of root production were anomalous. The anomalous estimates were attributed to a nonuniform labeling of tissue age classes resulting in differential decomposition/herbivory of ^{14}C:^{12}C through time, as well as movement and loss of labile ^{14}C through the first growing season. Isotope-dilution methodologies may be unreliable for any estimate of pool turnover when the labeling period is not as long as pool-turnover time.

Problems and biases associated with traditional harvest maxima-minima methods of estimating aboveground primary production are well known, but are greatly exacerbated when the method is used to estimate root production. Estimates of root production by ^{14}C dilution were unrealistic. ^{14}C turnover methodology provided reliable estimates of production in this community.

Key words: belowground turnover; crowns; decomposition; exudation; labile carbon; litter; root production; shortgrass steppe; soil carbon; structural carbon.

INTRODUCTION

Primary production is a fundamental concept in ecology, but estimates of net primary production (NPP) by current techniques are subject to serious bias and errors, particularly estimates of belowground NPP (BNPP) (Singh et al. 1975, 1984, Fairley and Alexander 1985, Milchunas et al. 1985, Hansson and Andrén 1986, Lauenroth et al. 1986, Kurz and Kimmins 1987, Sala et al. 1988). BNPP across biomes is currently estimated to range from 40 to 85% of total NPP, a major source of organic input to these ecosystems (Coleman 1976, Fogel 1985). However, the potential inaccuracy of BNPP estimates by the commonly used harvest maxima-minima methods can range from an overestimation as high as 700% in grassland ecosystems (Sala et al. 1988) to an undefined underestimation when no statistically significant maxima-minima are observed (Hansson and Andrén 1986, Kurz and Kimmins 1987, Fogel 1990). Maxima-minima methods are based on the assumption that biomass increases can be calculated by subtracting the minimum biomass at the start of a period from the maximum biomass at the end of the period. All date-to-date increases in biomass are then summed over a time series of samples (usually a year or a growing season), with the number of samples per date, the number of sample dates in the time series, and the manner of defining a significant increase dependent upon the investigator (Singh et al. 1984). Other methods such as root ingrowth, root observation, and nitrogen budget approaches also suffer from a variety of assumptions and problems. The ^{14}C dilution technique offers promise for avoiding many of the problems associated with traditional methods of estimating BNPP, but requires assumptions that have not been addressed in field studies (Caldwell and Camp 1974, Milchunas et al. 1985).

The ^{14}C dilution technique is based on the reduction of the ratio of ^{14}C:^{12}C after pulse-labeling when plants assimilate only new ^{12}C (Caldwell and Camp 1974). The turnover coefficient is expressed as $TC = [(^{14}C_{t1}/^{12}C_{t1})/(^{14}C_{t2}/^{12}C_{t2})] - 1$ where $t1$ and $t2$ are different

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sampling dates. The turnover coefficient can be based upon data for structural tissue (cell wall fiber), thereby eliminating potential error associated with seasonal translocation of labile ^{12}C between shoots and roots. BNPP is determined by multiplying TC of each component by the total biomass of the component at time 1. Results from a growth chamber experiment (Milchunas et al. 1985) indicated that incorporation of labile ^{14}C into structural tissue and dissipation via respiration and exudation in two species of grass require a complete growing season. Estimates of BNPP by ^{14}C dilution made prior to stabilization can result in negative turnover coefficients.

Sources of error associated with harvest maxima-minima estimates of production under field conditions include missing maxima and minima, missing individual species' maxima and minima, exaggerated maxima and minima due to sampling variance, growth after maxima, exudation and sloughing, decomposition and herbivory (Milchunas et al. 1985). By contrast, only three of the sources of error (exudation, decomposition, and herbivory) affect estimates of BNPP by ^{14}C dilution. An estimate of exudation can be obtained from pulse-labeling. All to none of the errors associated with decomposition and herbivory are incorporated into BNPP estimates by ^{14}C dilution. They could result in an overestimation, underestimation, or no effect, depending on the nonuniformity or uniformity of plant-^{14}C:^{12}C decomposition and herbivory rates due to potential differential labeling of tissue age classes. The effects of decomposition and herbivory on estimates of BNPP by ^{14}C dilution were not tested in our growth chamber experiment (Milchunas et al. 1985).

All methods of estimating BNPP mentioned thus far have a series of assumptions, and sources of error that are difficult to quantify. This raises the important question of how to evaluate estimates from various techniques when the true answer is not known. The long-term turnover of ^{14}C in various compartments provides a relatively unbiased estimator of turnover, albeit an integration over several years. This is because turnover will not be biased by differential decomposition or herbivory rates of plant ^{14}C:^{12}C. In contrast, turnover is directly based upon the life-herbivory-death-decomposition cycle of the ^{14}C-labeled plant tissue. Differences between production and decomposition (non-steady-state conditions) can be determined by the difference in standing crops between dates. An assumption of the ^{14}C turnover method is that the concentration of label is spatially uniform through the profile, but need not be uniform with respect to age class as long as the tissue is new and actively growing and the labeled tissue quality (potential decomposability) does not vary with time of labeling. Spatially uniform label concentrations may be maximized by labeling when there is moisture throughout the profile.

Our objectives were to compare estimates of BNPP obtained by harvest, ^{14}C dilution, and ^{14}C turnover methods, to evaluate the effects of sources of bias on the estimates, and to examine the partitioning of labile carbon in relation to its effects on estimates of BNPP.

Methods

The study was conducted at the Central Plains Experimental Range (40°49′ N, 104°46′ W), located in the northern portion of the shortgrass steppe region in northcentral Colorado, ≈56 km northeast of Fort Collins, Colorado. During the past 20 yr, mean annual precipitation has been 322 mm, ranging from 226 to 479 mm. Approximately 71% of the precipitation occurred during the May through September growing seasons. Mean monthly air temperatures ranged from 22°C in July to below 0°C in January. The vegetation is dominated by *Bouteloua gracilis* (H.B.K.) Lag., with *Opuntia polyacantha* Haw., *Sphaeralcea coccinea* (Pursh) Rydb., and *Artemisia frigida* Willd. as consistent components. Basal cover is typically 25–35%, 90% of which is *B. gracilis* (Milchunas et al. 1989).

Eight long-term and eight short-term plots were located in a level upland site that had been ungrazed since 1969. Each long-term plot was 3 × 3 m and each short-term plot was 2 × 2 m. Both short- and long-term plots had a 30 cm wide border that was not sampled, thereby preventing dilution from non-^{14}C-labeled plants outside the plot. *B. gracilis* roots rarely extend >20 cm horizontally from the edge of the canopy (Lee 1990). The remainder of each plot was divided into 64 squares for long-term plots or 36 squares for short-term plots. The location of squares within each plot was ascertained for each sampling date by stretching string between 20 cm long spikes permanently placed outside the plot.

Square, flat-topped plastic tents 46 cm in height and of the same area as the long- and short-term plots were constructed for ^{14}C labeling. Each of the tents had four electric swivel fans mounted on each side. The equivalent of a 20-mm rainfall event was applied 4 d prior to labeling to assure active aboveground photosynthesis and belowground root activity throughout the soil profile. A narrow border around each plot was cleared of vegetation to seal the clear plastic tent at the ground surface by covering it with soil.

Two plots were labeled each day in order to allow time for immediate sampling of short-term plots (to obtain estimates of total fixation) and because the 2-h labeling process had to be accomplished in mid- to late-morning so temperatures inside the tent could be maintained within the typical range of maxima. Initial inside air temperatures in the sun averaged 25°C, and reached 35°C outside and 45°C inside the tents at the end of labeling. A temperature of 45°C in the sun is approximately equivalent to a 30°C temperature in the shade, which is less than the high of 38°C in the shade that plants are often exposed to.

All short-term plots were labeled once with 9.25×10^7 Bq ^{14}C (2.5 mCi), during 2–5 July 1985. All of the

larger sized long-term plots were labeled twice, each plot with a total of 2.2×10^8 Bq ^{14}C (6 mCi), during 25–28 June and 9–12 July 1985. Two vials of $Na_2{}^{14}CO_3$ and two vials of $Na_2{}^{12}CO_3$ were placed in each tent. The vials were midway between the center of the plot and one of the four fans at each side, and were suspended above the canopy. This allowed thorough mixing of the air inside the tent and reduced leaf-boundary-layer resistance to insure efficient, uniform assimilation of $^{14}CO_2$. The tube portion of a thin-window Geiger-Müller (GM) counter was inserted into a hole in one of the tents and sealed. $^{14}CO_2$ was released from both vials of $Na_2{}^{14}CO_3$ by injecting H_2SO_4. The time at which GM-tube counts leveled off indicated that the CO_2 compensation point of *B. gracilis* had been reached ($\approx$150 μL/L CO_2). One vial of a quantity of $Na_2{}^{12}CO_3$ sufficient to raise CO_2 levels in the tent to 350 μL/L was then released. This was followed by a second CO_2 drawdown, release of another vial of $Na_2{}^{12}CO_3$, and a third drawdown. The GM-tube/compensation point method was useful in providing qualitative information about CO_2 uptake rates and helped achieve high labeling efficiency and uniformity across plots. However, 100% fixation of the $^{14}CO_2$ is impossible for many reasons.

Five randomly chosen squares in each of the eight plots were sampled on each date. Short-term plots were sampled immediately after removing the tent and 5, 35, 85, 267, 381, and 485 d after labeling, with the latter three dates representing early spring, peak live biomass, and late fall in 1986. Since all plots were not labeled on the same day, sampling was staggered whereby the number of days after labeling was uniform across plots. Long-term plots were sampled in spring and fall each year starting in 1986, one growing season after labeling, i.e., 267, 485, 632, 846, and 1013 d after labeling. With less frequent sampling in the future, we plan to sample these plots for another 10+ yr.

Two adjacent cores were removed from the center of each of 5 squares per plot (2 cores $\times$ 5 squares $\times$ 8 plots = 80 cores/date) for each of the short- and long-term groups of plots. The cores were 66.5 mm inside diameter, with one driven to 20 cm and one to 40 cm depth. Thus, only 9 and 13% of the square's area, for long- and short-term plots, respectively, were disturbed. Before driving the cores into the soil, we collected aboveground biomass, including litter. We mixed and subsampled each soil core, and washed roots from the remainder of the soil by the floatation method of Lauenroth and Whitman (1971) using a 0.5-mm mesh sieve. Coarse roots from the soil subsample were hand picked and fine roots removed by vacuum. The vacuum method entailed securing two layers of $\approx$0.5-mm mesh veil cloth over a vacuum nozzle and shaking the sample in a flat pan while holding the nozzle at a height whereby only fine roots were collected on the cloth. Vacuumed and floated roots were combined, and further fine sorting of all plant samples completed by hand. Sample categories on short-term plots were aboveground green tissue, dead plus litter, crowns, roots, and soil, and for long-term plots were aboveground plus litter, crowns, roots, and soil.

The 80 cores per sample date for each short-term and long-term experiment provided 80 aboveground and crown samples and 40 root and soil samples for each depth. Based on previous experience, we selected a sample size of 40 root samples to provide a low variance. This is especially important for calculating BNPP from harvest data because of the overestimation bias from artificial or exaggerated maxima and minima due to sampling variance. Estimates of cumulative mean biomass with increasing sample size generated from random sampling from 80 cores (0–20 cm) taken on the same date (a date on which both long- and short-term plots were sampled) indicated that a sample size of 40 cores provided estimates well within the 95% confidence interval (Fig. 1).

Plant material was oven-dried at 55°C, weighed, milled to pass a 1-mm mesh screen, and subsamples ashed at 550°C for expressing values on an organic matter basis. Soil samples were dried at 55°C and ground with mortar and pestle.

Eight sites were located $\approx$3 m north of each long-term set of plots for supplemental sampling of root biomass to 20 cm on additional dates through the growing season. Sampling intensities and sample preparations were the same as previously described, except that the entire root sample was ashed. These data, in conjunction with those from labeled plots, were used to calculate root production by harvest maxima-minima methods.

Cell wall constituents (CWC) of plant tissues were isolated to provide an estimate of structural material using a modification of the standard neutral-detergent fiber (NDF) procedure (Van Soest 1967, Van Soest and Wine 1967). We used a 0.1-g plant tissue sample with 20 mL neutral detergent solution and 0.4 mL decahydronaphthalene in test tubes topped with marbles and refluxed in a block digester. Residues were collected by centrifuging and removing supernatant with a disposable pipette connected to a vacuum, followed by three wash (hot water and acetone) and centrifuge cycles. The washed residue was dried at 55°C in the test tubes and scraped free with a spatula. This modification was necessary because it was impossible to filter crown and root samples due to clogging by tissue-bound soil contamination. Washed root samples typically ranged from 30 to 50% ash.

Whole-plant and CWC fractions were combusted in a Packard Model 305 tri-carb sample oxidizer, using Carbosorb as a trap and a Permafluor IV cocktail. ^{14}C activity was determined by liquid scintillation counting, with quench correction by an external standard. Soil carbon activities were assayed using the wet oxidation procedure of Snyder and Trofymow (1984) with carbon traps modified (ethylamine rather that NaOH)

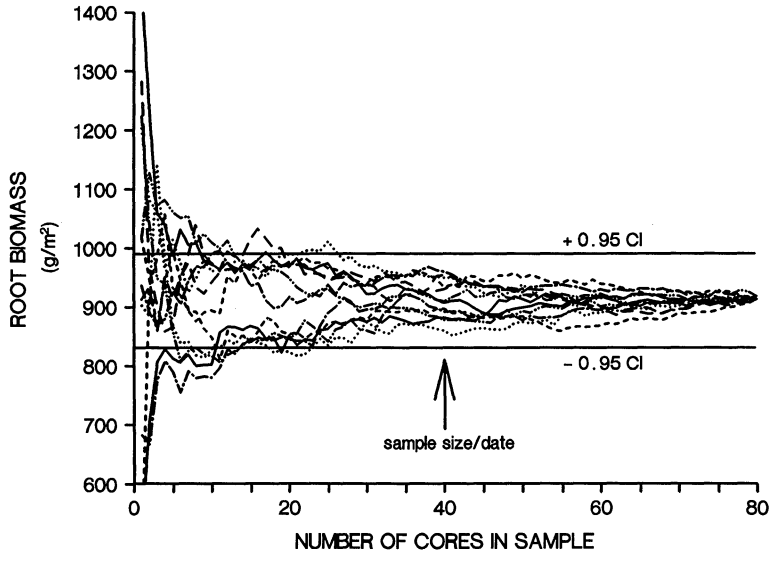

FIG. 1. Estimates of mean root biomass generated by randomly sampling 1 through 80 core samples (0–20 cm) for a date on which both short-term plots (40 cores) and long-term plots (40 cores) were sampled (Spring 1986). Each line represents a separate random sampling of the same 80 cores. The 95% confidence interval is from the HSD calculated from the analysis of variance for the 23 sample dates in Fig. 2.

for compatibility with a scintillation cocktail containing, per litre, 630 mL toluene, 370 mL methanol, 5 g PPO (2,5-diphenyloxazole), and 0.1 g POPOP [1,4-bis-2-(5-phenyloxazolyl)-benzene]. Plant material standards assayed with soil samples were within 1% of the values obtained by the dry-oxidation procedure, after quench correction.

A repeated-measures analysis of variance was used to evaluate time differences, plant part (and soil) differences, and the interaction between the two. The within-subjects factor was plant part, because plant part values were obtained from the same sampled square (core). The between-subjects factor was time, because new squares were randomly selected at each date. The individual squares were identified by plot, which played the role of block in the between-subjects analyses. The test of each effect (i.e., time, plant part, or plant part by time interaction) was performed by comparing the mean square for that effect to the mean square for the interaction of that effect with plot. This procedure yields the usual test for the between-subjects effect, and yields tests for within-subjects effect and interaction that are more conservative than a test based on individual squares. Individual squares were treated as subsamples in this analysis. The analysis was unbalanced because measurements from both cores in a square contributed to the aboveground and crown data, but only one core contributed to the root and soil data for each depth.

Pairwise comparisons of plant parts collected on the same date were made using Tukey's HSD method adjusted by Kramer for unequal sample sizes (Dunnett 1980). Pairwise comparisons of dates for the same plant part were made using Tukey's HSD method with error terms obtained from a separate between-subjects analysis of each plant part. Separate analysis by plant part makes the individual HSD comparisons more accurate if there are minor differences in error variances between plant parts.

RESULTS

Precipitation in the year of pulse labeling (1985) was the same as the 20-yr mean (320 mm), although the monthly distribution was different (Fig. 2). The year prior to labeling (1984) was a relatively wet year (407

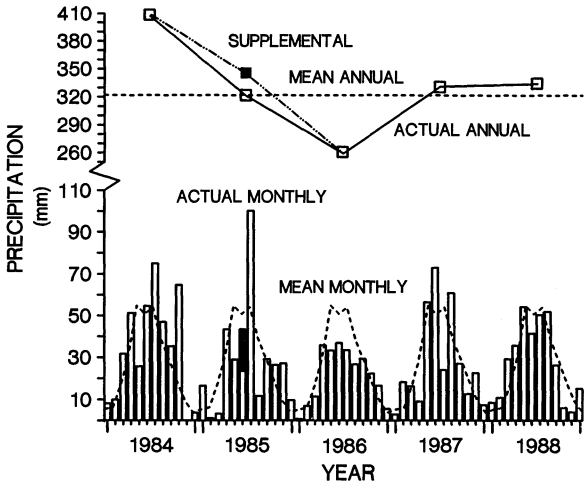

FIG. 2. Annual and monthly precipitation for 1984 through 1988 at the Central Plains Experimental Range, compared with long-term means (– – –). Solid black portions indicate supplemental watering.

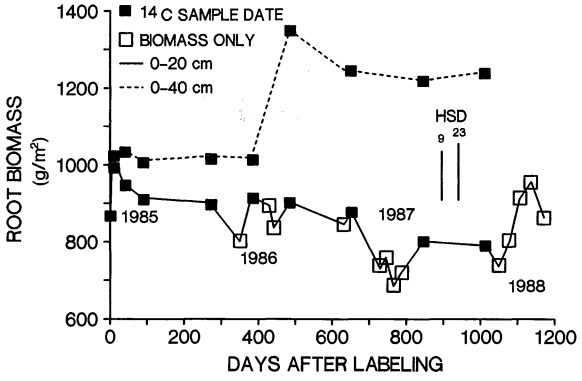

FIG. 3. Root biomass for 0–20 cm and 0–40 cm depths for 1985 through 1988. Each point is a mean of 40 cores. Use HSD_{23} to determine significant differences between dates within the 0–20 cm depth and HSD_9 for dates within the 0–40 cm depth.

mm), as were 1982 (479 mm) and 1983 (400 mm). Annual precipitation from 1982 to 1986 steadily declined, but was followed by 2 yr of average precipitation. Root biomass in the 0–20 cm depth (in grams per square metre) gradually declined [(root biomass = -0.21(no. days) + 949, $r^2 = 0.62$, $N = 19$)] during the 1985 through early 1988 interval (Fig. 3). In contrast, root biomass in the 0–40 cm depth remained stable from 1985 through mid-1986, increased over 300 g/m^2 by autumn of 1986, and remained at this higher level through spring 1988.

Carbon dynamics

The ^{12}C mass of perennial biomass components on the short-term plots was stable over time with the exception of a decrease in crown biomass during 1985 and an increase in 0–40 cm roots in late 1986 (Fig. 4A). On long-term plots, ^{12}C mass of 0–40 cm roots showed an increase during 1986 similar to that observed on short-term plots, then remained constant through 1988 (Fig. 4B). Other plant components were relatively stable through time. Averaged across all sample dates for the long-term plots, the distribution of ^{12}C mass among components was 116, 193, 386, and 527 g/m^2 for aboveground (standing live and dead plus litter), crowns, 0–20 cm roots, and 0–40 cm roots, respectively. Considering crowns as aboveground organs and using 0–40 cm roots, ≈60% of plant carbon in this grassland is belowground.

^{14}C in plants and the plant-soil system declined rapidly throughout the 1985 growing season (Fig. 5). After an 85-d stabilization period, ^{14}C declined at a slow and constant rate from the winter of 1985–1986 through the spring of 1988. There was a 79% loss of ^{14}C mass from day 0 to day 85 and only a 40% loss from day 267 to day 1013. For the two dates on which both short- and long-term plots were sampled (days 267 and 485), long-term plots contained an average of 33% more $^{14}C/m^2$ than short-term plots, even though long-term plots received only 16% more $^{14}C/m^2$. We anticipated a loss of efficiency in $^{14}CO_2$ uptake with multiple labeling, but thought this would be a trade-off with an increase in uniformity of label distribution. The higher ratio of atmospheric concentrations of $^{14}CO_2$ to $^{12}CO_2$ in long-term tents compared to short-term tents may have increased assimilation efficiencies, and with the use of three CO_2 drawdowns, overcome the effect of losses upon removing the tents. There was no difference between short- and long-term plots in the coefficient of variation of ^{14}C in plant or the plant–soil system, and no significant differences in the proportioning among biomass components.

The dynamics of ^{14}C within a component of the short-term plots were most rapid between days 0 and 35 (Fig. 6A). From day 0 to day 5, there was a large decline in live-leaf ^{14}C, a significant, but small, decline in crown ^{14}C, and significant increases in root and soil ^{14}C. Live-leaf ^{14}C mass continued to decline rapidly through day 85 (the autumn of the 1st yr). The largest decrease in crown ^{14}C occurred between day 5 and 35. Root and soil ^{14}C did not significantly change from day 5 through

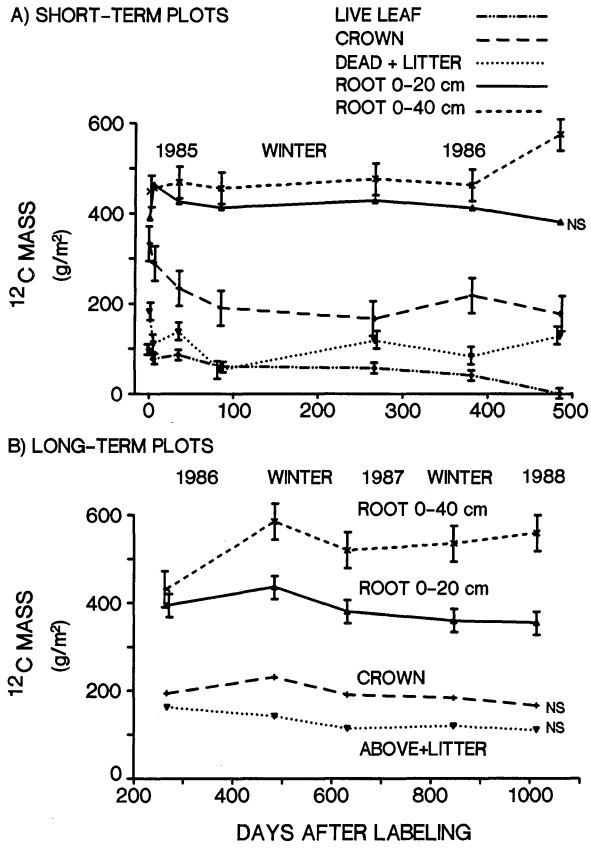

FIG. 4. ^{12}C mass through time of plant components for (A) short-term plots, and (B) long-term plots. Above + litter refers to aboveground standing live plus dead plus litter on the surface of the soil. HSD confidence intervals test for significant differences between sample dates within a plant component.

85, and dead-leaf-plus-litter ^{14}C increased between day 35 and 85 with the senescence of aboveground leaves. During the first winter after labeling, small declines were observed in all ^{14}C pools except for an increase in litter ^{14}C.

^{14}C pools in the year following labeling (1986) were stable with respect to crowns, roots, and soil (Fig. 6A, B). Significant changes in ^{14}C pools during the 2nd yr involved a decline in aboveground live biomass to near zero by midseason (peak standing crop) and a corresponding increase in litter (short-term plots). Aboveground biomass and litter were combined on long-term plots, and this pool decreased steadily during the second winter and the third growing season after labeling to only 4 $\mu g^{14}C/m^2$ by the third winter and fourth spring after labeling (Fig. 6B). A decrease in root ^{14}C started during the second winter after labeling. The decrease in root ^{14}C from the second spring to the fourth spring was 45% in 0–20 cm roots and 26% in 0–40 cm roots.

The cell wall fractions of the various plant parts ranged from 69 to 83% (Fig. 7A). Roots had a significantly higher proportion of cell walls than aboveground parts, litter, or crowns at the spring of labeling. Aboveground plant biomass was the only component that significantly changed through the growing season. The seasonal trend of declining cell wall proportion of roots and increasing cell wall proportion of other plant parts resulted in no significant differences between root and live-leaf components by the end of the growing season.

Cell wall ^{14}C masses of most components were dynamic throughout the year of labeling (Fig. 7B). For cell wall ^{14}C, aboveground mass decreased over time, root and litter mass increased over time, and crown mass increased from day 0 to 5 and remained constant thereafter. These changes in ^{14}C masses of the cell wall fraction can be due to movement of labile carbon to structural carbon within a plant part or to transfer of tissue from one pool to another. Significant amounts of labile ^{14}C were incorporated into cell walls of all components from day 0 to 5 and from day 5 to 35 (Fig. 7C). Small quantities of labile ^{14}C were still being transferred to cell wall components aboveground and in crowns between days 35 and 85, after pulse-labeling. The leveling-off of cell wall ^{14}C as a percentage of total ^{14}C (Fig. 7C) and of total plant ^{14}C mass (Fig. 5) suggests that stabilization of labile ^{14}C in the plant occurred by day 85 after pulse-labeling, with the majority occurring by day 35.

With the stabilization of labile ^{14}C established, we can obtain crude estimates of exudation and respiration losses from the plant. Total loss of ^{14}C was considered to be the result of respiration and exudation/sloughing, and was calculated as total ^{14}C mass uptake on day 0 minus plant ^{14}C mass at stabilization of labile ^{14}C. Exudation/sloughing was estimated as maximum soil ^{14}C mass during the labile ^{14}C stabilization period (the immediate increase between day 0 and 5), and

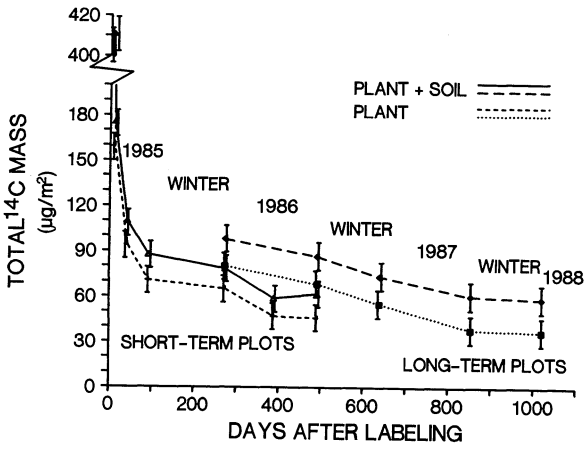

FIG. 5. Total ^{14}C mass in plant and plant plus soil from the time of pulse-labeling in 1985, through 1988, for both short- and long-term plots. HSD confidence intervals test for significant differences between sample dates within plant or within plant + soil component.

respiration was estimated as total loss minus exudation/sloughing. Estimates indicated (1) total losses were 77% of initial ^{14}C uptake, (2) exudation and sloughing were 4% of initial system ^{14}C and 17% of plant stable ^{14}C, and (3) respiration loss was 73% of initial uptake. These estimates used day 35 as the labile ^{14}C stabilization date because the small increases in the cell wall percentage ^{14}C may introduce less error into the estimates than possible decomposition/herbivory losses from peak standing crop (day 35) to autumn (day 85). However, estimates using day 85 as the labile ^{14}C stabilization date were similar to those obtained using day 35, i.e., 83, 4, 24, and 78%, respectively.

Estimates of net primary production

Estimates of ANPP, crown net primary production (CNPP), and BNPP were obtained by harvest, ^{14}C dilution, and plant part turnover of ^{14}C mass (^{14}C turnover). NPP estimates by harvest are presented from this study as well as other studies in which similar ungrazed level uplands were sampled.

BNPP estimates by the harvest method were calculated using various statistical constraints to identify significant increases in biomass (Table 1). BNPP for 2 out of 4 yr was not statistically different from zero using the conservative ANOVA error term and conservative means separation test of this study. Estimates using the same data but other statistical constraints were significantly positive for all 4 yr, and the estimates were intermediate between those based upon ANOVA-HSD constraints and no statistical constraints. The highest estimate of BNPP using no statistical constraint was 56% less than the estimate of Sims and Singh (1978), which used a t test constraint, more frequent coring through the season, but fewer cores per date.

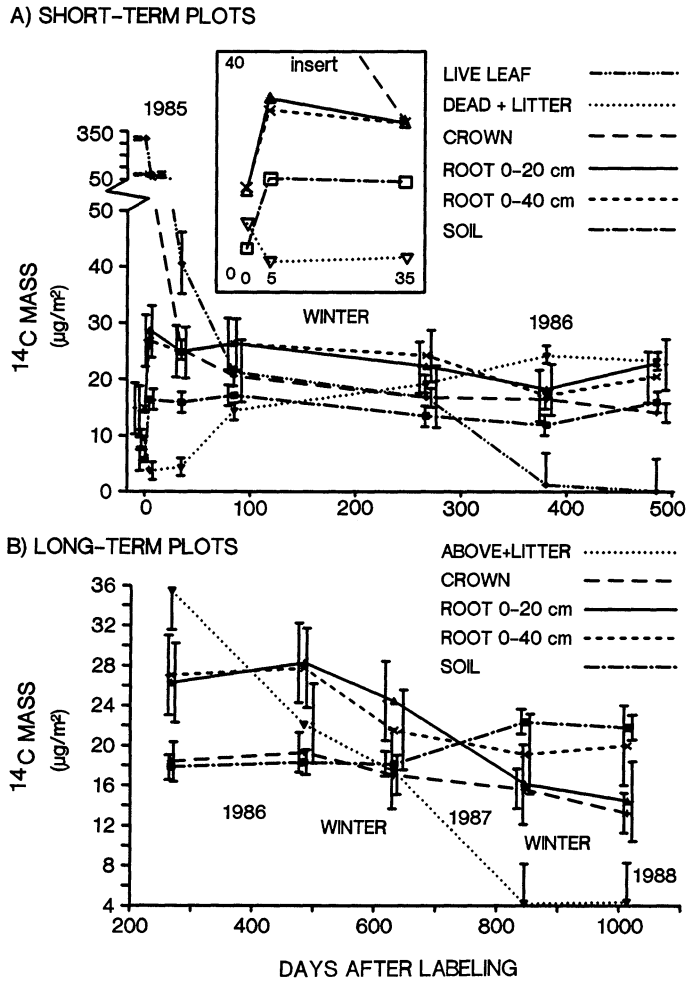

FIG. 6. ^{14}C mass through time of plant components and soil for (A) short-term plots, and (B) long-term plots. Above + litter refers to aboveground standing live plus dead plus litter on the surface of the soil. HSD confidence intervals test for significant differences between sample dates within a plant or soil component.

ANPP estimates based upon peak standing crop averaged 105 g/m^2 from 1985 to 1988 compared with an average of 128 g/m^2 from 1970 to 1974 for estimates based upon the sum of maxima of species groups through the growing season, and an average of 178 g/m^2 from 1970 to 1972 for estimates based upon the sum of species' maxima (Table 1). Methods of calculating ANPP vary across studies, but the years of measurement and years of exclosure to cattle grazing also vary. The only estimate of CNPP was 225 g/m^2 averaged over 2 yr.

Estimates of production by ^{14}C dilution were made for all plant components based on date-to-date and year-to-year intervals using both plot and overall means. Estimates of production by ^{14}C dilution during the 1st yr were heavily biased by respiration and exudation/sloughing losses and translocation within the plant prior to stabilization of labile ^{14}C (Table 2). For example, aboveground production from day 0 to day 5 was estimated to be $\approx$500 g/m^2, reflecting the large losses of ^{14}C to respiration and translocation to belowground organs. The increase in root ^{14}C mass from day 0 to day 5 resulted in estimates of BNPP ranging from -308 to -435 g/m^2. Estimates based on cell wall fractions of plant parts or cell walls corrected for increases in ^{14}C between dates did not resolve the problem of anomalous values (data not shown). Contrary to expectations, estimates of production by ^{14}C dilution continued to be anomalous for time intervals after stabilization of labile ^{14}C. Negative turnover coefficients and negative production estimates were obtained in several instances. The negative estimates after stabilization of labile ^{14}C occurred during over-winter periods, periods from peak standing crop to autumn, or for aboveground plant components. Annual ANPP estimates that were negative during the first 2 yr were positive for the 3rd and 4th yr, reaching a high of 709 g/m^2/yr for 1987–1988 compared with a harvest peak-standing-crop es-

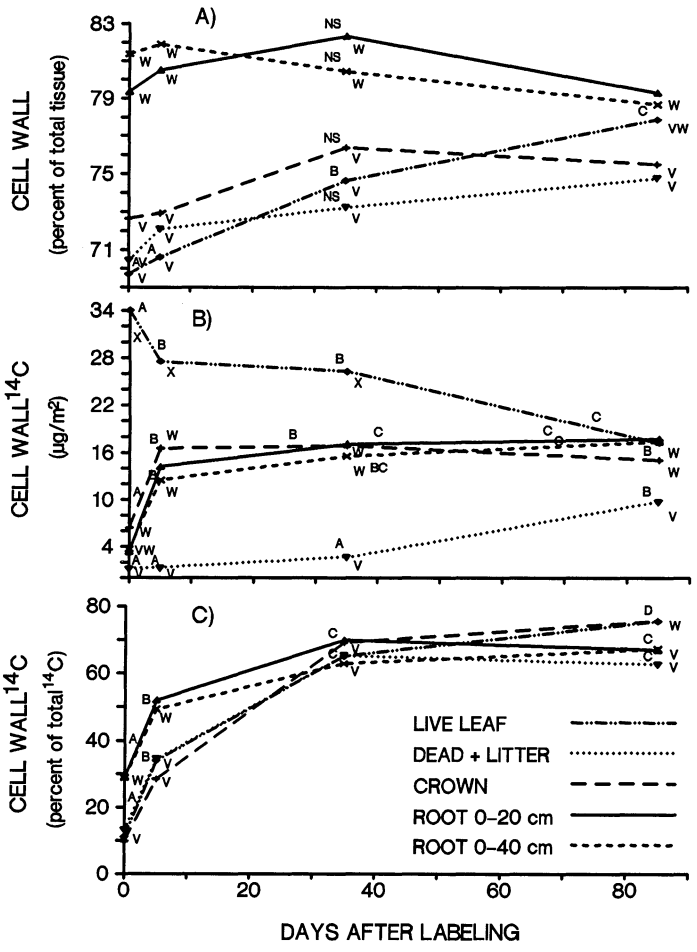

FIG. 7. Cell wall (A) percent of total tissue, (B) ^{14}C mass, and (C) ^{14}C percent of total ^{14}C for plant components through the first growing season after pulse-labeling. Dead + litter refers to aboveground standing dead plus litter on the surface of the soil. Sample dates within a plant component not sharing a common letter (A, B, C, or D) and plant components within a sample date not sharing a common letter (V, W, or X) are significantly different. NS = not significant with respect to sample dates.

timate of only 75 g/m²/yr. Estimates based on plot means (8 plots—5 root cores or 10 aboveground and crown cores per plot) had very large confidence intervals (see variance for 5 cores, Fig. 1). However, the estimates based on plot means were similar to those using overall means, and the 40 or 80 cores per date represented a large sample size.

A series of hypothetical situations was generated to assess potential factors contributing to the anomalous NPP values obtained by ^{14}C dilution (Table 3). Under conditions of proportional ^{14}C to ^{12}C losses (decomposition/herbivory) and holding ^{12}C gain (actual production) constant, the error associated with ^{14}C estimates of NPP increased with increasing rates of decomposition. Under conditions of proportional ^{14}C to ^{12}C decomposition and holding decomposition constant, increasing levels of actual production had no effect on the error associated with estimates of NPP by ^{14}C dilution. When ^{12}C decomposition was greater than ^{14}C decomposition and actual production was held constant, the same relationship of increasing error associated with increasing decomposition occurred as when ^{14}C and ^{12}C decomposition was proportional, but the magnitude and rate of increase of the error was greater and the sign was reversed. When ^{12}C decomposition was greater than ^{14}C decomposition and decomposition was held constant, error in the estimate of NPP decreased with increasing levels of actual production. However, when ^{14}C and ^{12}C losses were proportional and actual production to decomposition were held constant, increased proportional rates of decomposition and actual production in relation to standing biomass resulted in increased error in the estimate of NPP by ^{14}C dilution.

Estimates of turnover coefficients by ^{14}C turnover were obtained by regression of ^{14}C mass of plant parts over time, and calculation of the x intercepts. Annual estimates of ANPP, CNPP, and BNPP were calculated by dividing the mean biomass for the year by the estimated number of years required for complete turn-

TABLE 1. Net primary production estimates obtained by harvest methods for the Central Plains Experimental Range.

Plant part—method	Net primary production ($g \cdot m^{-2} \cdot yr^{-1}$) (Apr–Sep precipitation)					
A) Current study	1985 (237 mm)	1986 (195 mm)	1987 (250 mm)	1988 (260 mm)		Mean (236 mm)
Root (0–20 cm)*						
Maxima-minima						
ANOVA-HSD† ($P = .05$)	162	0	0	221		96
t test ($P = .05$)	162	115	116	221		154
1 SD	162	182	116	221		170
No statistics	162	182	174	221		185
Aboveground						
Peak standing crop‡						
With shrubs	128	119	80	91		105
Without shrubs	112	94	75	83		91
B) Dodd and Lauenroth (1979)	1970 (172 mm)	1971 (254 mm)	1972 (265 mm)	1973 (243 mm)	1974 (179 mm)	Mean (223 mm)
Aboveground						
Sum of maxima§						
With shrubs	182	114	166	121	59	128
Without shrubs	115	82	85	62	44	78
C) Sims and Singh (1978)	1970 (172 mm)	1971 (254 mm)	1972 (265 mm)			Mean‖ (260 mm)
Aboveground						
Sum of species maxima¶	160	218	138			172
Crown						
Maxima-minima‖		215	235			225
Root (0–20 cm)						
Maxima-minima‖#		471	372			422

* Sum of positive increments.
† Conservative error term and conservative means separation test (HSD using Tukey Q table).
‡ Peak standing crop current-year biomass from 15 0.25-m^2 clip plots in same area as ^{14}C plots (W. K. Lauenroth and D. G. Milchunas, *unpublished data*). HSD with $P = .05 = 24$ g/m^2.
§ Sum of peak standing crops of warm and cool season grasses and forbs, with shrubs as max-min; clip every 3 wk through the growing season.
‖ Using t test with $P = 0.05$; sampled every 2 wk through the growing season.
¶ Sampled every 2 wk through the growing season.
# Maxima-minima for each depth increment summed.

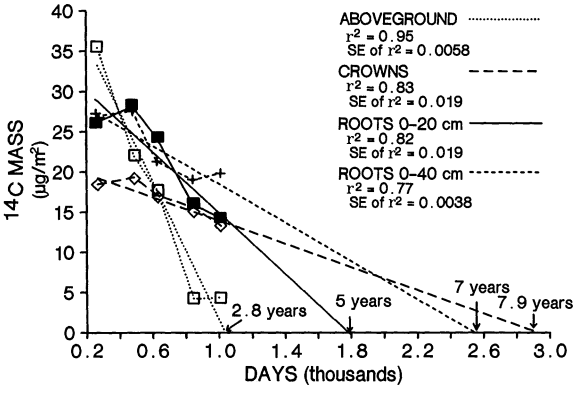

FIG. 8. Regression of ^{14}C mass on time, and extrapolations to time of complete turnover of ^{14}C, in plant components. Sample points are from long-term plots after stabilization of labile ^{14}C, i.e., 1986–1988, not including 1985.

over. The estimated number of years required for complete turnover was 2.8 yr for aboveground, 7.9 yr for crowns, 5 yr for 0–20 cm roots, and 7 yr for 0–40 cm roots (Fig. 8). Estimates of production by ^{14}C turnover averaged 108, 57, 175, and 151 $g \cdot m^{-2} \cdot yr^{-1}$ for aboveground, crown, 0–20 cm roots, and 0–40 cm roots, respectively (Table 4). Average aboveground to belowground ratios were near one when crowns were included in the aboveground fraction, and were 0.6 and 0.7 for 0–20 cm and 0–40 cm depths when crowns were excluded from the ratios.

The deviation of estimates of production by harvest maxima-minima, harvest peak crop, and ^{14}C dilution from those obtained by ^{14}C turnover indicates close agreement between aboveground estimates by harvest peak crop and ^{14}C turnover (Table 5). Compared with ^{14}C turnover, aboveground harvest peak crop under-

TABLE 2. Net primary production (g/m^2) and turnover coefficients (in parentheses) obtained by the ^{14}C dilution method for the Central Plains Experimental Range. Values within a plant part not sharing a common superscript letter are significantly different.

	A) Date (n) to date (n + 1)					
Days after ^{14}C labeling	0–5	5–35	35–85	85–267	267–381	381–485 267–485
Year	1985	1985	1985	1986	1986	1986
Season	Spring	Spring	Autumn	Winter	Spring	Autumn Summer
	Using core means within plots					
Aboveground	498^{c} (2.23)	182^{ab} (1.14)	68^{a} (0.33)	3^{a} (<0.01)	355^{bc} (2.79)	... ...
Litter	212^{d} (0.53)	20^{bc} (0.13)	−147^{ab} (−0.45)	−1.3^{abc} (0.04)	−152^{a} (−0.56)	121^{cd} (0.77)
Above + litter						116^{a} (0.60)
Crown	49^{a} (0.10)	517^{b} (0.87)	14^{a} (0.08)	37^{a} (0.07)	130^{a} (0.40)	−27^{a} (−0.04) 60^{a} (0.24)
Root 0–20 cm	−308^{a} (−0.34)	112^{b} (0.12)	−77^{ab} (−0.09)	217^{b} (0.24)	222^{b} (0.25)	−87^{ab} (−0.10) 50^{a} (0.08)
Root 0–40 cm	−435^{a} (−0.43)	146^{b} (0.13)	−57^{ab} (−0.03)	222^{bc} (0.19)	548^{c} (0.51)	67^{b} (0.05) 365^{a} (0.38)
	Using overall core means†					
Aboveground	501 (2.30)	173 (1.02)	61 (0.32)	−23 (−0.18)	169 (1.36)	... ...
Litter	242 (0.60)	11 (0.04)	−147 (−0.48)	−13 (−0.11)	−148 (−0.57)	121 (0.67)
Above + litter						151 (0.43)
Crown	90 (0.12)	490 (0.76)	<0 (0.00)	30 (0.07)	123 (0.33)	−24 (−0.05) 59 (0.14)
Root 0–20 cm						−240 (−0.26)
	−346 (−0.40)	59 (0.06)	−82 (−0.09)	207 (0.23)	167 (0.18)	
						25 (0.03)
Root 0–40 cm	−435 (−0.44)	110 (0.11)	−85 (−0.08)	135 (0.13)	395 (0.37)	41 (0.04) 278 (0.29)

	B) Year to year				
	Using core means within plots†				Using overall core means†
Day	0–267	85–485	267–632	632–1013	0–267
Year	Spring 85–Spring 86	Fall 85–Fall 86	Spring 86–Spring 87	Spring 87–Spring 88	Spring 85–Spring 86
Aboveground	−13^{a} (−0.06)	−39^{a} (−0.30)			−95 (0.24)
Above + litter			104^{a} (0.64)	696^{b} (2.81)	
Crown	733^{a} (1.08)	154^{b} (0.36)			822 (1.11)
			47^{a} (0.13)	67^{a} (0.15)	
Root 0–20 cm	−261^{a} (−0.27)	246^{b} (0.29)			−249 (−0.29)
			55^{a} (0.08)	573^{b} (0.70)	
Root 0–40 cm	−331^{a} (−0.32)	730^{b} (0.72)			−349 (−0.35)
			463^{b} (0.49)	220^{a} (0.19)	

* Mean annual of 2 yr: Spring 1986 through Spring 1988 for long-term plots.

† Core means within plots: eight plots used as replicates in ANOVA; overall core means: one mean value with no plot factor and no statistics possible.

TABLE 2. Continued

A) Date (n) to date (n + 1)			
485–632 1987 Winter	632–846 1987 Summer	846–1013 1988 Winter	Mean annual*
Using core means within plots			
... ...	... ...	... ...	
1[a] (0.02)	849[b] (3.30)	−41[a] (−0.11)	463 (1.90)
−32[a] (−0.05)	21[a] (0.09)	36[a] (0.11)	43 (0.19)
28[a] (0.04)	515[a] (0.65)	91[a] (0.11)	342 (0.44)
201[a] (0.15)	232[a] (0.20)	18[a] (<0.01)	408 (0.37)
Using overall core means†			
6 (0.02)	829 (3.26)	−29 (−0.11)	478 (1.80)
−34 (−0.07)	16 (0.04)	27 (0.07)	34 (0.09)
8 (0.01)	366 (0.43)	81 (0.10)	240 (0.29)
190 (0.15)	182 (0.16)	0 (0.00)	325 (0.30)

B) Year to year			
Using overall core means†			
85–485 Fall 85–Fall 86	267–632 Spring 86–Spring 87	632–1013 Spring 87–Spring 88	Mean annual*
−42 (−0.36)			
	95 (0.45)	709 (2.45)	402 (1.45)
150 (0.36)			
	26 (0.06)	45 (0.11)	36 (0.09)
58 (0.06)			
	32 (0.04)	488 (0.58)	260 (0.31)
627 (0.62)			
	459 (0.48)	182 (0.16)	321 (0.32)

estimated production by 16 to 18% and aboveground harvest maxima-minima overestimated production by 75%. Harvest estimates of production for belowground organs can only be made by maxima-minima. BNPP estimates by harvest maxima-minima ranged from −43 to +160% of those obtained by ^{14}C turnover, and CNPP was +353% of that estimated by ^{14}C turnover. Compared with ^{14}C turnover, ^{14}C dilution overestimated ANPP by 359%, underestimated CNPP by 28%, and overestimated BNPP by 64%. There were large standard deviations for aboveground and crowns in the annual deviations of estimates between ^{14}C dilution and ^{14}C turnover. The proportioning of production between aboveground, crowns, and roots (0–20 cm) was 22, 27, and 51% by harvest maxima-minima, 58, 5, and 37% by ^{14}C dilution, and 32, 17, and 51% by ^{14}C turnover.

DISCUSSION

Results from a growth chamber experiment that examined the implications of short-term carbon dynamics for estimates of BNPP by ^{14}C dilution (Milchunas et al. 1985) suggested that a modification of the original ^{14}C dilution technique (Caldwell and Camp 1974), whereby initial sampling occurred after stabilization of labile ^{14}C, would provide accurate estimates of BNPP. Our current field experiment does not support the conclusions from the growth chamber experiment. Our first objective in this discussion is to examine the similarities and differences between the two experiments, and to reexamine the assumptions involved in estimating NPP by ^{14}C dilution. This may provide insight into the contrasting conclusions from the two experiments. A second objective is to examine the potential sources of error and bias in estimates of NPP by ^{14}C turnover. In the process of meeting these objectives, we also assess the dynamics of carbon respiration, exudation, and death–decomposition in this shortgrass steppe site.

Differences in the growth chamber and the field during labeling and subsequent plant growth, and in carbon dynamics between the systems may both, or interactively, affect conclusions regarding estimates of NPP. In the growth chamber, *B. gracilis* plants were grown from seed and planted in field soil that had been dried, stored, and sieved to remove all old root and detrital material. How did these differences affect short-term dynamics of carbon?

Stabilization in the partitioning of labile ^{14}C from aboveground to crowns and roots was more rapid in the growth chamber (Milchunas et al. 1985) than in the field, although the majority of translocation to roots occurred by day 5 in both situations. The temporal dynamics of the incorporation of labile ^{14}C into structural material were very similar under both growth chamber and field conditions, requiring one complete growing season.

Estimates of respiration and exudation/sloughing were lower under growth chamber vs. field conditions (28 vs. 73% and 9 vs. 17%, respectively). Plant phenologies at labeling were similar in the growth chamber and field experiments, although plant maturities and attributes of the growth medium were very different. Biondini et al. (1988) estimated exudation of 15% for *B. gracilis* seedlings grown in fritted clay and nutrient solution, with no difference in exudation between *B. gracilis* grown with or without the presence of a rhizosphere microflora. Chung and Trlica (1980) reported (1) respiration values of 37–63%, with higher values observed at higher temperatures and a more advanced stage of phenology, and (2) 21–37% of the ^{14}C remained in the labile fraction at 28 d after labeling, with higher percentages in the labile fraction with lower temperatures and a more advanced stage of phenology. Our estimates of respiration and exudation/sloughing were obtained indirectly by calculations. Exudation/sloughing is probably underestimated (Milchunas et al. 1985), and respiration, calculated by subtraction, is probably overestimated due to incorporation of all other unaccounted for losses. For example, the very high rainfall the month after labeling (Fig. 2) may have leached soluble carbon from leaves, and root recovery by floatation may have leached soluble carbon from roots.

The combined results of these experiments suggest that (1) estimates of exudation based upon tracer methods may vary widely within a plant species due to a variety of biotic and abiotic factors, and (2) stabilization of labile carbon following labeling requires approximately one growing season. The long residence time of labile ^{14}C indicates that estimates of NPP based upon any carbon tracer methods should be made only after allowing one growing season for dissipation of the labile pool. However, there is a potential problem of not accounting for rapid turnover of labeled tissue (such as root hairs) that occurred during the dissipation of labile ^{14}C.

Estimates of production by ^{14}C dilution after the dissipation of the labile ^{14}C pool were sometimes negative and sometimes absurdly large. Although absolute production is not known, we can place reasonable bounds on aboveground production by the harvest method, with much less certainty on crown and root production. We know that harvest at peak standing crop underestimates ANPP (Lauenroth et al. 1986). In this grassland, however, the underestimation of ANPP by harvest at peak crop may not be large because of (1) the short growing season, (2) the dominance of warm-season species, and (3) the dominance of warm-season or total biomass by one species (*B. gracilis*). We also know that harvest maxima-minima overestimates ANPP and the overestimation can be large (Singh et al. 1984, Lauenroth et al. 1986, Sala et al. 1988). ANPP in 1988 by ^{14}C dilution was 10 times the estimate by peak crop and 437% greater than the highest estimate of ANPP by maxima-minima. The large overestimation of ANPP by ^{14}C dilution leads us to doubt estimates of CNPP and BNPP by ^{14}C dilution, where an acceptable range of values from harvest methods is not known.

Hypothetical situations indicated that differential decomposition and/or herbivory of ^{14}C:^{12}C, the magnitude of decomposition/herbivory, and the magnitude of decomposition/herbivory and production relative to standing biomass can influence estimates of NPP by ^{14}C dilution (Table 3). Caldwell and Camp (1974) considered the possibility that changes in the proportion of living and dead roots between sample dates may affect turnover coefficients. For two cool-desert shrub communities, they assumed a "rather small" underestimation of the turnover coefficient occurred because of the low proportions of dead roots and slow decomposition rates. Our results indicate that both over- and underestimation of production by ^{14}C dilution can occur, and the magnitudes of error in either direction can be large.

There are three possible explanations for the failure of the ^{14}C dilution technique. First, labile ^{14}C is translocated to only functional tissues (Ueno et al. 1967, Singh and Coleman 1973, 1974). The incorporation of labile ^{14}C into structural tissue is probably proportional to growth rate of a particular organ, i.e., sink demand (Swanson et al. 1976, Milchunas et al. 1982). Actively growing roots are probably young, and die and decompose later than roots that received less or no ^{14}C. Second, root biomass generally declined during the course of this study, indicating high rates of death-decomposition-herbivory relative to production. Third, aboveground standing biomass was small, and belowground biomass large, in relation to turnover mass. This would tend to result in greater error in estimates of ANPP than in estimates of BNPP. The very accurate estimates of production by ^{14}C dilution obtained in pot experiments (Caldwell and Camp 1974, Milchunas et al. 1985), with high carbon gain by seedlings and very low decomposition/herbivory losses, are exactly the conditions under which accurate estimates of production by ^{14}C dilution are expected. These conditions are unlikely to occur in the field, and the degree to which they do will not be known.

The potential for nonuniform labeling has implications for any tracer study that relies on isotope dilution. Turnover of ^{14}C-labeled roots in this study suggests that 8 yr of labeling would be required before a "uniform" label would be attained. Even under conditions of uniform labeling, the direction of the system in terms of carbon gain or loss would bias estimates of production by dilution calculations.

The limitations of isotope dilution methods do not necessarily extend to studies tracing the temporal movement of pulse labels through system compartments. In the case of production estimates by ^{14}C turnover, labeled roots advance through all stages of growth, survival, herbivory, death, and decomposition, and the turnover coefficient is based upon an integration over all stages. Annual estimates (turnover coefficient × be-

TABLE 3. Hypothetical ^{14}C decomposition and ^{12}C decomposition and production, compared with ^{12}C production calculated by ^{14}C dilution.

Initial ^{14}C mass	^{14}C loss	Initial ^{12}C mass	Actual ^{12}C loss	Actual ^{12}C gain	^{12}C gain by ^{14}C dilution	% error
			Proportionately equal ^{12}C loss to ^{14}C loss			
10	1	1000	100	100	111	11
10	2	1000	200	100	125	25
10	3	1000	300	100	143	43
10	4	1000	400	100	167	67
10	1	1000	100	200	222	11
10	2	1000	200	200	250	25
10	3	1000	300	200	286	43
10	4	1000	400	200	333	67
10	1	1000	100	300	333	11
10	2	1000	200	300	375	25
10	3	1000	300	300	429	43
10	4	1000	400	300	500	67
10	1	1000	100	400	444	11
10	2	1000	200	400	500	25
10	3	1000	300	400	571	43
10	4	1000	400	400	667	67
10	0.25	1000	25	50	51	3
10	0.5	1000	50	50	53	5
10	0.75	1000	75	50	54	8
10	2.5	1000	250	500	667	33
10	5	1000	500	500	1000	100
10	7.5	1000	750	500	2000	300
			Proportionately greater ^{12}C loss to ^{14}C loss			
10	0.5	1000	100	100	53	−47
10	1	1000	200	100	0	−100
10	1.5	1000	300	100	−59	−159
10	2	1000	400	100	−125	−225
10	0.5	1000	100	200	158	−21
10	1	1000	200	200	111	−44
10	1.5	1000	300	200	59	−71
10	2	1000	400	200	0	−100
10	0.5	1000	100	300	263	−12
10	1	1000	200	300	222	−26
10	1.5	1000	300	300	176	−41
10	2	1000	400	300	125	−58
10	0.5	1000	100	400	368	−8
10	1	1000	200	400	333	−17
10	1.5	1000	300	400	294	−26
10	2	1000	400	400	250	−38

ginning biomass) can be adjusted by the increase or decrease of biomass by the following year to account for inequalities in production to decomposition/herbivory, but differences in decomposition/herbivory for the year of estimate from the mean decomposition/herbivory rate would cause error. This error would be a fraction of that obtained by the root harvest technique (where no estimate of decomposition/herbivory is possible), and the magnitude would be the actual value of the difference in the amount of decomposition/herbivory for that year from the mean. Thus, estimates by ^{14}C turnover may be sensitive to atypical climate years. An additional assumption of the ^{14}C turnover method is that the age class and quality (decomposability) of the labeled material will not vary with time of labeling. This may be minimized by labeling the same plots several different times during the growing season.

While the assumptions of the ^{14}C turnover method appeared to not be violated to any large degree in this study, additional testing in other plant communities will be necessary before the validity of the method can be accepted. Advantages of the method are that no artificial environments are created for the production-decomposition/herbivory processes to occur under; disadvantages are the time required to conduct the experiment (several years). Advances in ^{13}C technology will eliminate problems associated with the handling of radioactive ^{14}C. The use of minirhizotrons is another promising technique for root turnover and production studies (Taylor 1987), although many assumptions and potential limitations of this technique also require further testing (McMichael and Taylor 1987, Cheng et al. 1990).

Our estimates of ANPP by ^{14}C turnover were between those obtained by harvest peak crop and harvest maxima-minima, even though the decay function was extrapolated to predict the time of complete turnover. Moreover, the 16–18% underestimation by harvest peak crop, and the 75% overestimation by harvest maxima-minima compared with ANPP estimates by ^{14}C turn-

TABLE 4. Net primary production (NPP) and aboveground to belowground NPP ratios obtained by the ^{14}C turnover method for the Central Plains Experimental Range.

	NPP by ^{14}C turnover ($g \cdot m^{-2} \cdot yr^{-1}$)					
	1985*	1986*	1986†	1987†	1988†	Mean
Aboveground	159	111	94	93	87	109
Crown	74	52	60	53	47	57
Root (0–20 cm)	188	180	185	165	158	175
Root (0–40 cm)	145	160	143	149	157	151
	Aboveground : belowground ratios					
0–20 cm with crowns‡	1.24	0.91	0.83	0.88	0.85	0.95
0–20 cm without crowns	0.86	0.62	0.51	0.56	0.55	0.62
0–40 cm with crowns‡	1.61	1.02	1.08	0.98	0.85	1.10
0–40 cm without crowns	1.10	0.69	0.66	0.62	0.55	0.73

* Mean biomass from short-term experiment plots divided by number of years for complete turnover.
† Mean biomass from long-term experiment plots divided by number of years for complete turnover.
‡ Crowns included in aboveground fraction.

over are reasonable considering that we know harvest peak crop underestimates ANPP, and harvest maxima-minima can potentially overestimate ANPP by even much greater percentages. The apparent reliability of ANPP estimates by ^{14}C turnover, and the use of composite live, dead, and litter components in deriving the turnover coefficients, provide some confidence in the estimates for belowground organs, where we are much less confident about estimates resulting from harvest data.

Previous CNPP and BNPP estimates by harvest maxima-minima for this shortgrass steppe site (Sims and Singh 1978) were +353% and +160% of estimates obtained by ^{14}C turnover. Data for nine other grassland sites across North America (Sims and Singh 1978) suggest an overwhelming importance of belowground carbon inputs for grassland systems. However, estimates of BNPP by ^{14}C turnover from this field study, and the demonstration by simulation modelling (Singh et al. 1984, Lauenroth et al. 1986) and mathematical analyses (Sala et al. 1988) of the potential for overestimation by harvest maxima-minima, suggest that belowground inputs of carbon may be less than that indicated from previous estimates.

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TABLE 5. The deviation of the mean estimate of NPP by harvest or ^{14}C dilution from the mean estimate by ^{14}C turnover, and the deviation of the annual estimates of NPP by harvest or ^{14}C dilution from the annual estimates by ^{14}C turnover.

Method Plant part	Deviation of mean from ^{14}C turnover mean* (%)	Deviation of mean from annual turnover* (%)	
		Mean	SD
Harvest			
Current study			
Root (0–20 cm) ANOVA-HSD	−45	−43†	69
Root (0–20 cm) no statistics	6	13	23
Aboveground peak crop‡	−16	−16	11
Dodd and Lauenroth (1979)			
Aboveground peak crop	−28	−18§	26
Sims and Singh (1978)‖			
Aboveground	63	75¶	32
Crown	295	353¶	67
Root (0–20 cm)	141	160¶	35
C^{14} dilution¶			
Aboveground	269	359	504
Crown	−37	−28	33
Root (0–20 cm)	49	64	205

* $[(\text{Mean method}_x - \text{mean } C^{14} \text{ turnover})/\text{mean } C^{14} \text{ turnover}] \cdot 100$, or; $[(\sum_{\text{yr } 1}^{n} (\text{previous for } x))]/n$.

† Considering years of zero production as 100% error.
‡ Without shrubs. See Table 1 footnotes.
§ Matching years of similar precipitation.
‖ Sum of positive increments without shrubs. See Table 1 footnotes.
¶ Using year-to-year estimates by mean of all cores for long-term plots.

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