Observations on biomass dynamics of a crested wheatgrass and native shortgrass ecosystem in southern Wyoming

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Abstract

Above- and belowground net primary production (ANPP and BNPP) were compared between a 30-year-old crested wheatgrass site and an adjacent native shortgrass prairie. ANPP was estimated using successive harvests in May, June, July, and October 1985. BNPP was estimated using soil cores to a depth of 100 cm at the same time that aboveground harvests were made. ANPP was significantly greater in the crested wheatgrass site compared to the native site, but belowground and total net primary production were not different. The native shortgrass system, however, had greater live root biomass early in the growing season. The crested wheatgrass system had a high accumulation of aboveground dead material at the start of the growing season, which was followed by a significant decline in June and an increase in July and October. The native shortgrass system, however, had significantly lower accumulations of aboveground dead material. Approximately 92% of the fixed carbon in the native site was allocated belowground, while crested wheatgrass allocated about 85% of its fixed carbon belowground.

Key Words: aboveground production, belowground production, standing dead litter, *Agropyron cristatum,* blue grama, western wheatgrass

Large areas of abandoned croplands in the western U.S. were seeded with crested wheatgrass [*Agropyron cristatum* (L) Gaertn.] during the 1930's (Rogler and Lorenz 1983). More than a million hectares were seeded with this species in both Montana (Woolfolk 1951) and Canada (Smoliak and Dormaar 1985). Some of these communities have remained virtual monocultures for more than 50 years without apparent successional trends (Vallentine 1971).

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This work was supported by National Science Foundation grant NSF/BSR-8405604. The authors wish to thank Titki-D. Tarassoum for his assistance in data collection.
Manuscript accepted 22 September 1988.

Earlier studies by Brown and Trlica (1977a, b), Detling (1979), Kemp and Williams (1980), Caldwell et al. (1981), and Monson et al. (1983) on photosynthesis and carbon allocation have shown major differences in carbon and nutrient allocation for crested wheatgrass and 2 major components of the shortgrass steppe, blue grama [*Bouteloua gracilis* (HBK) Lag.] and western wheatgrass (*Agropyron smithii* Rydb.). Power (1980) and Smoliak and Dormaar (1985) have shown differences in production between native grassland sites and crested wheatgrass communities, while Sims et al. (1978) and Sims and Singh (1978 a,b) have reported differences in plant structure and function between warm- and cool-season species in major grassland types in North America.

The objective of this study was to make a detailed comparison in the: (1) dynamics of above- and belowground live and dead biomass; (2) dynamics of litter deposition; and (3) above- and belowground net primary production between a stable 30-year-old crested wheatgrass monoculture and an adjacent native shortgrass prairie.

Methods

Study Site

The High Plains Grassland Research Station (HPGRS) is a USDA-ARS research station located 7 km west of Cheyenne, Wyo. The topography of the area is nearly level to undulating at an elevation of about 1,900 m. The soil of the experimental areas is an Ascalon fine, loamy, mixed mesic Aridic Arguistol (Young and Singleton 1977). The climate is semiarid-temperate with an average growing season of 120 days. The average annual temperature is 9° C with extremes ranging from 42° C to –36° C. Precipitation averages 365 mm with recorded extremes of 159 to 544 mm. Approximately 78% of the precipitation falls between 1 April and 30 September.

Blue grama is the dominant warm-season species in the native site, while western wheatgrass, needle-and-thread (*Stipa comata* Trin. & Rupr.), junegrass [*Koleria cristata* (L.) Pers.], and Sand-

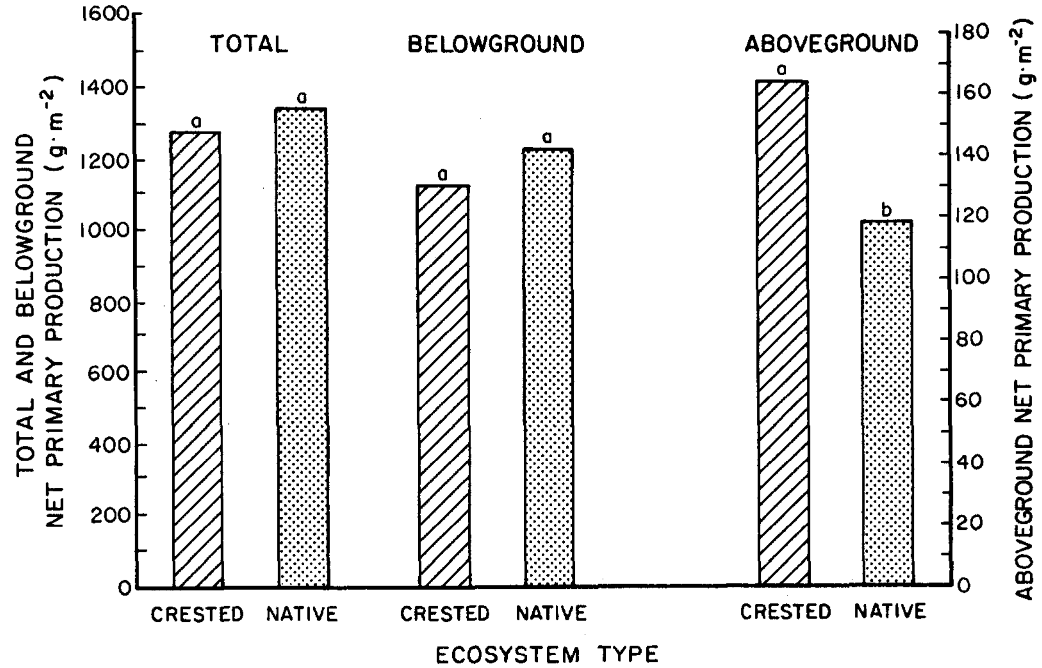

Fig. 1. *Aboveground, belowground, and total net primary production for crested wheatgrass and native shortgrass ecosystems. Different letters denote significant differences at* $P \leq 0.01$. *Data collected in 1985 in southeastern Wyoming.*

berg bluegrass (*Poa secunda* Presl.) are the principal cool-season grasses.

The crested wheatgrass site, located within 0.8 km of the native site, was plowed in the 1930–1940 period and used for research plots for many years. The site was seeded to crested wheatgrass in the early 1950's and has not been tilled since that time. This site is still virtually a monoculture even though it is surrounded by native shortgrass prairie. Both sites were grazed at a moderate level in the past, but were fenced to exclude livestock grazing prior to this study.

Design

The total size of each research area was about 0.3 ha. Four adjacent blocks were established in both the native shortgrass and the nearby crested wheatgrass systems in October 1984. Rectangular (1.5×32-m) plots within each block served as basic experimental units for vegetation sampling. The study was conducted as a randomized complete block design with 4 replications in each plant community.

Sampling

Above- and belowground vegetation sampling was conducted throughout the 1985 growing season. Successive harvests were made in May, June, July, and October in both the native shortgrass and crested wheatgrass ecosystems. The July harvest date represented peak production based on phenological stage of development and root growth using the root periscope technique described by Richards (1984). Harvests were made utilizing 10 rectangular sample plots (0.4 × 1.25 m) randomly located in each plot.

Standing crop samples were clipped to ground level, and live material was separated by major species. Standing dead and litter were collected and treated as separate components. All samples were oven dried at 60° C for 48 hr before weighing.

Belowground biomass was estimated using 5-cm diameter cores. One core was taken from each sample plot to a depth of 1 m. Cores were divided into 5 depths in the crested wheatgrass system (0–5, 5–10, 10–20, 20–60, and 60–100 cm) and 4 depths in the native shortgrass system (0–5, 5–10, 10–30, and 30–100 cm). Root cores were divided differently for the 2 ecosystems because of differences in soil horizonation that resulted from plowing the crested wheatgrass site in the 1930's. Root samples were removed from the soil using a modified hydropneumatic elutriation system (Smucker et al. 1982). Root samples were separated into live and dead components using color and friability as the primary basis for separation. In addition, a subsample of roots from 1 core per block at each sampling date was placed in a 10-ml solution of 0.1% 2,3,5-triphenyl tetrazolium chloride (TTC) to better distinguish live and dead roots (Jacques and Schwass 1956). Root samples in TTC solution were incubated in the dark at room temperature for about 16 hr before separation. The basis for this technique is that live root cells reduce TTC (colorless) to formazan (red), while dead roots lack the ability to reduce TTC and therefore remain unstained. All roots were oven dried at 60° C for 48 hr before weighing. Root samples were ashed in a muffle furnace at 1,000° C for 5 hr and then re-weighed to express root biomass on an ash free basis.

Above- and belowground net primary production (ANPP and BNPP) were estimated following Sala et al. (1981a):

$$ANPP = \sum_{i=1}^{n} P_i + S_c + F_c \text{ where:}$$

P_i = positive differences in 2 successive measurements of aboveground live biomass for species i. If the difference was negative, the value calculated was called specific net senescence (S_i).

S_c = correction factor to account for the senescence process. It represents the increment of standing dead material not accounted for by the summation of individual species specific net senescence ($\sum_{i=1}^{n} S_i$).

It consists of material that was produced but did not generate an increase in live biomass because it occupied the place left by material which was senesced during the same period. S_c is calculated as:

$$S_c = \Delta^+ \text{standing dead} - \sum_{i=1}^{n} S_{ci}$$

F_c = correction factor to account for the decay process. It represents the increase in litter not accounted for by the decrease in standing dead. F_c is calculated as:

$$F_c = \Delta^+ \text{litter} + \Delta^- \text{standing dead}$$

BNPP = RP + RS_c where:

RP is the belowground equivalent of $\sum_{i=1}^{n} P_i$

RS_c is the belowground equivalent of S_c

Analyses

The data were analyzed using a modified split-plot ANOVA model with system in the whole plot and depth and date in the sub-plot. To account for auto-correlation of dates and depths, the degrees of freedom for depth and date were reduced after ANOVA (Geisser and Greenhose 1958, 1959). Tukey's Honest Significance Difference (HSD) or an F-protected LSD were used following a significant F-ratio at the $p \leq 0.05$ and $p \leq 0.10$ respectively.

Results

Aboveground net primary production (ANPP) was significantly greater in the crested wheatgrass system compared to the native shortgrass system (Fig. 1). Belowground net primary production (BNPP) and total net primary production (TNPP), however, did not differ between the 2 sites (Fig. 1).

Aboveground live biomass increased in the crested wheatgrass system between May and July to a peak of 114 g/m², declining later to a low of 20 g/m² in October (Fig. 2). Aboveground live biomass

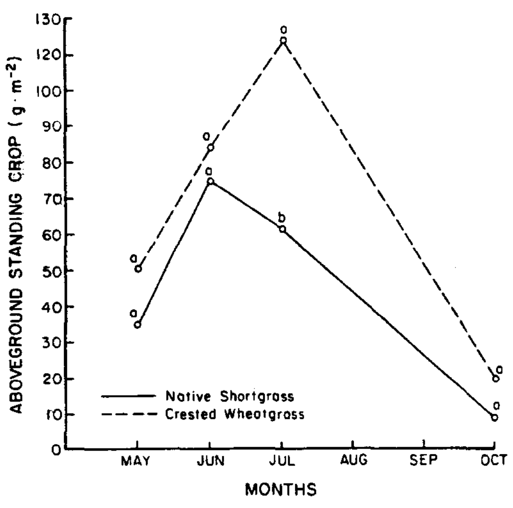

Fig. 2. *Aboveground live biomass for crested wheatgrass and native shortgrass ecosystems. Different letters denote significant differences at P≤0.05. Data collected in 1985 in southeastern Wyoming.*

in the native shortgrass ecosystem followed a similar pattern, but peaked in June at 75 g/m² (Fig. 2). The only significant difference in aboveground biomass between the 2 ecosystems was found in July (Fig. 2).

The native shortgrass ecosystem allocated approximately 8% of its fixed carbon to aboveground biomass, while the crested wheatgrass system allocated about 15% of its fixed carbon aboveground.

The standing dead component of each ecosystem followed a similar trend throughout the growing season (Fig. 3). The amount of standing dead in the crested wheatgrass system declined significantly during the first half of the growing season and then increased during the last half of the season. Standing dead was

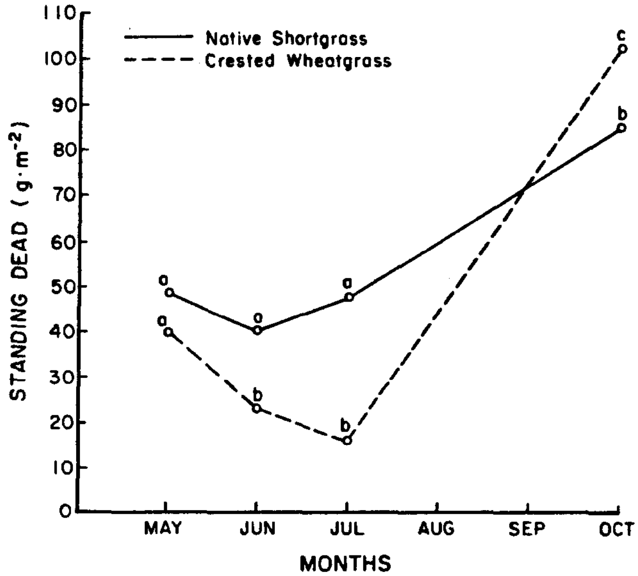

Fig. 3. *Standing dead biomass for crested wheatgrass and native shortgrass ecosystems. Different letters denote significant differences at P≤0.05. Data collected in 1985 in southeastern Wyoming.*

similar between the 2 systems in May and significantly lower in the crested wheatgrass ecosystem in June and July. At the end of the season, the crested wheatgrass system had significantly more standing dead than the native system (Fig. 3).

Litter accumulation was significantly greater in the crested wheatgrass system compared to the native system throughout the growing season (Fig. 4). There was little variation in the amount of litter present in the native shortgrass system between May and October.

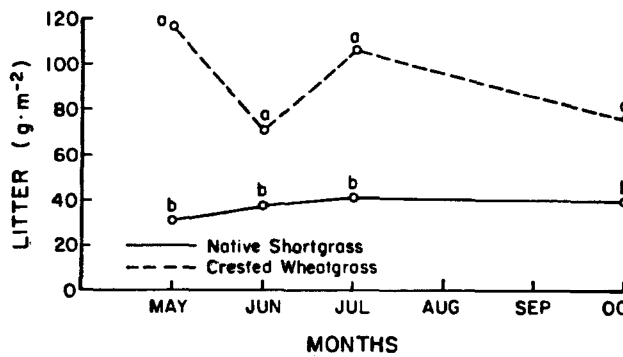

Fig. 4. *Litter production in crested wheatgrass and native shortgrass ecosystems. Different letters denote significant differences at P≤0.10. Data collected in 1985 in southeastern Wyoming.*

Belowground live biomass was significantly greater in the native shortgrass ecosystem than in the crested wheatgrass system only at the start of the growing season (Fig. 5). Beginning in June, both systems followed similar trends (Fig. 5). Approximately 85% of the fixed carbon in the crested wheatgrass system was allocated below-

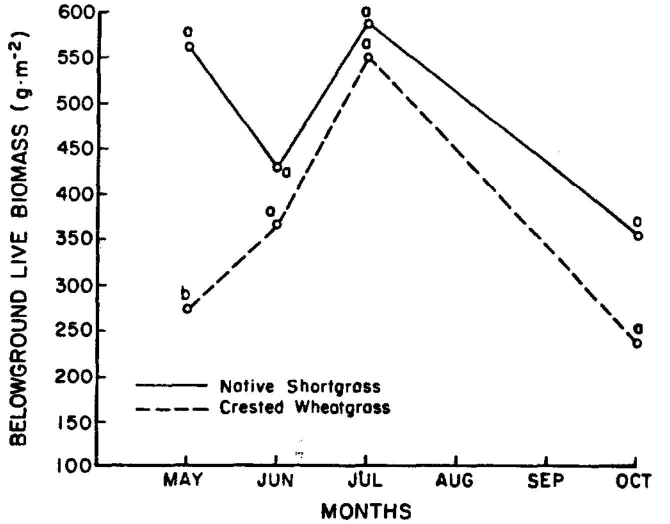

Fig. 5. *Belowground live biomass for crested wheatgrass and native shortgrass ecosystems. Different letters denote significant differences at P≤0.10. Data collected in 1985 in southeastern Wyoming.*

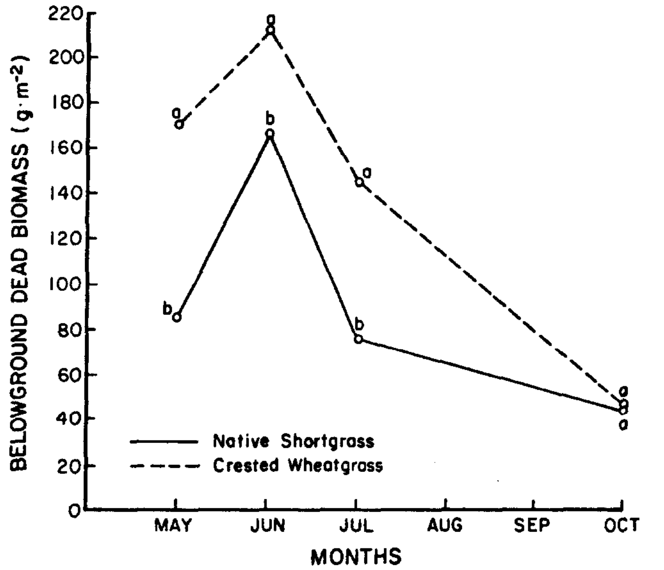

Fig. 6. *Belowground dead biomass for crested wheatgrass and native shortgrass ecosystems. Different letters denote significant differences at P≤0.05. Data collected in 1985 in southeastern Wyoming.*

ground, while the native system allocated belowground about 92% of the carbon it fixed during the growing season.

The dead component of the root mass was significantly greater in the crested wheatgrass system than the native system at each sampling period except in October (Fig. 6). Both systems followed similar trends with an increase in belowground dead material between May and June, followed by a steady decline until the end of the growing season.

Table 1 shows live root dynamics by depth within the 2 ecosystems. The pattern of root growth in the crested wheatgrass system was the same at all depths throughout the growing season (Table 1). Root biomass increased between May and July and then declined to the lowest level in October. The native shortgrass ecosystem displayed a different pattern or root growth in that there was an initial decline in root biomass at all but the deepest depth between May and June (Table 1). This was followed by an increase in root mass at all but the deepest depth between June and July. Root biomass then declined at all depths between July and October.

Discussion

The purpose of this study was to document differences in the structure and function of primary producers between a 30-year-old crested wheatgrass ecosystem and an adjacent native shortgrass prairie. The data idicate that the 2 systems differ in ANPP with the crested wheatgrass system having greater ANPP than the native system. However, BNPP was expected to be greater in the native system than the crested wheatgrass ecosystem as hypothesized by Power (1980) and Smoliak and Dormarr (1985), but this was not the case. In this study the crested wheatgrass site had BNPP and TNPP that was similar to the native site. Although BNPP was not different between the 2 systems, the native ecosystem had significantly greater live root biomass early in the growing season. This may be an indication that the major plant species in the native ecosystem were able to maintain a larger proportion of live roots during the winter period than did crested wheatgrass, or that the

Table 1. Belowground live biomass (g m^{-2}) by depth for the native and crested wheatgrass systems. Data collected in 1985 in southeastern Wyoming.

	Native Ecosystem							
Depth	May		June		July		October	
(cm)	$\bar{x}$	(SE)*	$\bar{x}$	(SE)	$\bar{x}$	(SE)	$\bar{x}$	(SE)
0–5	183	(44)	75	(32)	166	(47)	90	(65)
5–10	107	(55)	68	(22)	136	(50)	79	(34)
10–30	152	(28)	100	(36)	156	(9)	114	(41)
30–100	118	(36)	186	(133)	129	(41)	74	(36)
	Crested Wheatgrass Ecosystem							
Depth	May		June		July		October	
(cm)	$\bar{x}$	(SE)*	$\bar{x}$	(SE)	$\bar{x}$	(SE)	$\bar{x}$	(SE)
0–5	79	(21)	88	(13)	160	(77)	40	(10)
5–10	61	(20)	103	(94)	140	(35)	67	(30)
10–20	58	(5)	71	(42)	76	(42)	60	(13)
20–60	47	(20)	97	(54)	125	(87)	53	(23)
60–100	30	(17)	38	(38)	52	(16)	17	(8)

*SE = Standard error

native system actually began root production earlier in the season than crested wheatgrass.

Peak aboveground standing crop occurred in July for crested wheatgrass and June for the native ecosystem. Since the native ecosystem was dominated by a C_4 grass (blue grama) and the crested wheatgrass site was dominated by a C_3 species, we hypothesized that the native site would show peak production in July and the crested wheatgrass site in June (Kemp and Williams 1980). If total standing crop (above- and below-ground) is considered, both systems peaked in July, which was a result of the unusually high precipitation received at both sites in July (110 mm).

The crested wheatgrass ecosystem had a higher accumulation of aboveground dead material (standing dead and litter combined) in May, which was followed by a significant decline in June and an increase in July and October. This is compared with lower accumulations of aboveground dead material in the native ecosystem and minimal seasonal variation in litter accumulation. The lignin to nitrogen (N) ratio of the aboveground litter and total N immobilized in dead material were significantly higher in the crested wheatgrass system than in the native ecosystem (Ingham et al. 1988). Lower quality litter has lower decomposition rates and therefore may account for the higher accumulation of dead material in the crested wheatgrass system throughout the growing season. This lower quality litter may need to be weathered over winter before it will be rapidly decomposed by soil microflora. This mechanism may explain the pulse type decomposition even (reduction in standing litter) observed in early June (Fig. 4). The higher quality litter in the native ecosystem (Ingham et al. 1988, Uresk et al. 1975), on the other hand, may produce a more stable and constant decomposition rate, resulting in even distribution of litter throughout the growing season as was observed in the native system (Fig. 4). If this "pulse" vs. "even" decomposition hypothesis is true, then one can predict that the crested wheatgrass ecosystem may be more N limited than the native ecosystem at certain times of the growing season. Preliminary evidence in support of this hypothesis has been provided by Klein et al. (1987) with data that show net microflora N immobilization in the crested wheatgrass system but no immobilization in the native ecosystem in June 1985.

Power (1980) and Smoliak and Dormaar (1985) have shown that a substantial amount of carbon (70 to 80%) is allocated to the roots of native species such as blue grama, while crested wheatgrass allocated more carbon to the aboveground photosynthetic tissue. Our studies confirm even greater proportions in that the native system allocated approximately 92% of its carbon belowground and the crested wheatgrass system allocated about 85%. The crested wheatgrass system allocated nearly twice the amount of carbon to photosynthetic tissue than plants in the native ecosystem.

Approximately 74% of the root mass in the native system was found in the upper 30 cm while 68% of the root mass in the crested wheatgrass site was found in the upper 20 cm. This compares to a 75 to 90% range for both crested wheatgrass and native mixed prairie reported by Power (1980) for similar depths. Peak root growth for crested wheatgrass occurred in July at all depths, which corresponds to the wettest month of the growing season. The native shortgrass site displayed a different pattern of root growth when compared to crested wheatgrass and appeared to be more sensitive to the low amount of precipitation received between the May and June sampling (53 mm). The decline in root production during this period at all depths above 30 cm and an increase in root production at depths below 30 cm indicates that water may have been limiting root production in the native site at shallow depths during the later half of May and first half of June. Trlica and Biondini (1989) have shown that soil water depletion on this native shortgrass site was greater at shallower soil horizons than the crested wheatgrass site throughout the 1985 growing season. This suggests that the decline in root growth in the native ecosystem at depths less than 30 cm was due to lower precipitation during mid May to mid June.

The results from this study indicate that the 2 systems differ in biomass allocation and dynamics in the year studied. These differences and the persistence of both ecosystems might well represent alternative stable states that allow these 2 systems to exist under similar environmental conditions. Plant species from the native system have had little success in displacing crested wheatgrass over the past 30 years and crested wheatgrass has essentially been confined to the area originally seeded.

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