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Weathering losses of forage species on the fescue grassland in southwestern Alberta

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Willms, W., King, J. and Dormaar, J. F. 1998. **Weathering losses of forage species on the fescue grassland in southwestern Alberta**. Can. J. Plant Sci. **78**: 265–272. Rough fescue grasslands are readily damaged by heavy grazing pressure in the summer but tolerate grazing in winter. The grasslands have physical and nutritive properties that make them suitable for winter grazing by cattle thereby reducing the cost of winter feeding while preserving the integrity of the grasslands. However, their forage value declines during winter through the degradation of biomass yield and quality. This study took place at the Agriculture and Agri-Food Canada, Range Research Substation located on the Porcupine Hills in southwest Alberta. The objectives of this study were to determine the dynamics of litter biomass for important forage species over winter, to examine the role of leaf position in the plant on biomass loss from leaves, and to determine the associated changes in crude protein, phosphorus, and acid detergent fibre of the leaves, and carbon and nitrogen. Leaves of Parry oat grass (*Danthonia parryi* Scribn.), Idaho fescue (*F. idahoensis* Elmer), and rough fescue (*F. campestris* Rydb.) were sampled at monthly intervals from August to March over 3 yr to determine weight and chemical composition. Decomposition of these species, together with smooth aster (*Aster laevis* L.), was also tested for decomposition in the litter mass using nylon bags. Degradation of standing litter was most rapid in late summer and tended to decline toward stability by December. Biomass losses in leaves from August to March were similar ($P > 0.05$) among grass species. Overwinter losses in the litter mass tended to be greatest for smooth aster. Changes in the mineral and fibre concentrations of the herbage were typical of the trends expected for the period, that included late senescence and weathering, and followed closely the losses of biomass for the period. Forage decomposition is an important ecological process in mineral cycling and affects the quantity and quality of forage available for delayed grazing.

Key words: Standing litter, buried litter, biomass, forage quality, winter, Parry oat grass, Idaho fescue, rough fescue, smooth aster

Willms, W. D., King, J. et Dormaar, J. F. 1998. **Pertes par altération des espèces fourragères dans les herbages à fétuque du sud-ouest de l'Alberta**. Can. J. Plant Sci. **78**: 265–272. Les grands parcours à fétuque rude sont facilement endommagés par un pâturage intensif en été, mais ils supportent bien le pâturage d'hiver. Ces parcours possèdent les propriétés physiques et nutritives qui les rendent aptes aux pâturages d'hiver pour les bovins, réduisant d'autant le coût d'affouragement en hiver tout en préservant l'intégrité du peuplement herbager. Il reste que leur valeur fourragère baisse durant l'hiver, à la fois en quantité qu'en qualité. Nos expériences avaient lieu à la Sous-station de recherches sur les parcours (ministère de l'Agriculture et de l'Agroalimentaire du Canada) dans les Porcupine Hills au sud-ouest de l'Alberta. Nos objectifs étaient d'établir la dynamique de la formation de la litière à partir des espèces fourragères importantes durant l'hiver, d'examiner le rôle de la position des feuilles sur la tige sur les pertes de biomasse foliaire et d'élucider les modifications concomittantes des teneurs en protéine brute, en P et en lignocellulose des feuilles ainsi que celle du bilan du carbone et de l'azote. Les feuilles de la danthonie de Parry (*Danthonia parryi* Scribn.), de la fétuque de l'Idaho (*F. idahoensis* Elmer) et de la fétuque rude (*F. campestris* Rydb.) étaient prélevées tous les mois à partir d'août jusqu'en mars pendant 3 ans, pour en mesurer le poids et la composition chimique. La décomposition de ces espèces ainsi que celle de l'aster lisse (*Aster laevis* L.) étaient également mesurées dans la litière au moyen de sachets de nylon. La dégradation de la litière sur pied était particulièrement rapide en fin d'été, pour graduellement atteindre un niveau stable en décembre. Les déperditions de biomasse foliaires d'août à mars étaient du même ordre ($P > 0{,}05$) pour toutes les espèces de graminées. Les déperditions hivernales au profit de la litière étaient particulièrement fortes chez l'aster lisse. L'évolution des teneurs en minéraux et en fibres de l'herbage concordaient avec les attentes pour la période, prenant en compte la sénescence avancée et l'altération en place, et elles suivaient de près l'évolution des pertes de biomasse durant la période. La décomposition des plantes fourragères est une étape écologique importante dans la transformation des minéraux et elle influe sur la quantité et sur la qualité des ressources fourragères disponibles pour la fin de la période de paissance hivernale.

Mots clés: Litière sur pied, litière enfouie, biomasse, qualité fourragère, hiver, danthonie de Parry, fétuque de l'Idaho, fétuque rude, aster lisse

The climax communities of the foothills rough fescue grasslands are dominated by rough fescue (*Festuca campestris* Rydb.). Rough fescue is displaced by Parry oat grass (*Danthonia parryi* Scribn.) and other associated species on more xeric sites and with heavy grazing pressure (Willms et al. 1985). However, rough fescue tolerates grazing while dormant, and appears to be a suitable species for winter grazing since it is a tufted, "hard" grass with a large stature that maintains its quality better than other forage species in this community (Johnston and Bezeau 1962). These characteristics are particularly important in winter when forage quality is low and snow cover reduces availability.

Abbreviations: ADF, acid detergent fibre; **CP**, crude protein; **P**, phosphorus

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The cost of delayed grazing until winter is not only in the potential loss of forage quality but also of forage biomass that degrades and disappears. Altai wildrye (*Elymus angustus* Trin.) leaves lost 41 and 52% of their biomass from October to March in 2 different years, respectively (Willms 1991). In rough fescue communities, biomass losses over winter were up to 60% of total biomass present in October but losses differed between grasses and forbs (Willms et al. 1996). Therefore, the species composition of the grassland is important in determining the proportion of biomass that is lost and is an important consideration in determining the value of grasslands that are used for winter grazing.

Senesced vegetation may be either standing or decumbent but both are part of the litter component in grasslands. At least a portion of decumbent litter becomes buried and compacted by the weight of snow during winter. Although standing litter is more accessible to herbivores, decumbent litter represents a large proportion of biomass on grasslands that will be utilized by livestock when forage supply is limited.

Nutrients and biomass are lost from leaves by redistribution of nutrients within the plant, fragmentation through weathering, leaching (1977), and photochemical (Moorhead and Reynolds 1989) and microbial degradation (Holland and Coleman 1987). Differences in decomposition among plant materials can be accounted for largely by labile mineral content (Hunt 1977). Therefore, the rate of loss is greatest following senescence and is partly defined by species that vary in chemical composition.

Plant material degradation may continue throughout the winter under snow (Bleak 1970) and during warm periods (Hunt 1977). Decomposition of the aerial component is primarily by fungi, which are more resistant to water stress than bacteria; however, decomposition by fungi is slower than by bacteria because fungi are limited by nitrogen (Holland and Coleman 1987). However, nitrogen concentration in herbage can increase as a result of immobilization by microbes (Subhash and Ramakrishnan 1988; Shariff et al. 1994) or a loss of carbon by respiration (H. Janzen, personal communication) leading to an apparent improvement in forage quality.

Forage degradation is an important process that has significant implications for winter grazing. The differences in response among species are not well understood but is an important factor that defines the value of a community for winter grazing. Therefore, a study was made to investigate biomass degradation over winter to test the hypothesis that the cost of delayed grazing was species dependent. The objectives of this study were to determine the dynamics of litter biomass for important forage species over winter, to examine the role of leaf position in the plant on biomass loss from leaves, and to determine the associated changes in CP, P, and ADF of the leaves, and carbon and nitrogen. The material used in this study consisted of senesced leaves (litter) that had been produced in previous growing season.

METHODS

The study was conducted 85 km northwest of Lethbridge near Stavely (50°12′, 113°57′; 1350 m above sea level) in the Porcupine Hills of southwestern Alberta. The area consisted of two sites that were about 1 km apart and had been protected from grazing for the previous 10 yr. Samples were collected in each of 3 successive years beginning in 1992.

Soils are classified as thin Orthic Black Chernozemic developed on till overlying sandstone. The grassland vegetation is representative of the Rough Fescue Association described by Moss and Campbell (1947).

Changes in Biomass

1. Standing litter. In each year of the study, five plants of rough fescue, Idaho fescue (*Festuca idahoensis* Elmer), and Parry oat grass, were randomly selected at monthly intervals from August to March at each of two sites on rough fescue grassland. Five leaves were sampled at each of five, within-plant locations, defined by the quadrants north, south, east, and west, and the plant centre. Leaf position within the plant of these tufted species may affect their exposure to wind and, therefore, their degradation. The leaves were cut near their base, their lengths measured, oven-dried, and weighed.

All subsequent calculations were based on a standardized, 1-cm leaf unit which was determined by calculating the average unit weight, calculating the regression coefficients of unit weight on leaf length and adjusting for a 20-cm leaf length. This adjustment was necessary because the unit weight was significantly ($P < 0.05$) affected by leaf length. The adjustment was made by calculating regressions for each year, month, and species combinations and applying them to their respective observations.

2. Nutritive constituents. The current years' herbage production of rough fescue, Idaho fescue, Parry oat grass, and smooth aster (*Aster laevis* L.) was sampled from a random selection of at least five plants of each species at monthly intervals from August to March. A composite sample of each species was dried at 50°C, and ground through a laboratory mill equipped with a 1-mm screen in preparation for chemical analyses.

The herbage samples were analyzed for ADF according to the Association of Official Agricultural Chemists (1984) method 7.076 using filter paper instead of sintered glass crucibles, CP by colorimetric determination of Kjeldahl nitrogen (×6.25) using the Technicon Auto Analyzer II (Technicon Instruments Corp., New York, NY), and for P according to Ward and Johnston (1962).

Changes in Buried Litter

Senesced herbage samples of rough fescue, Idaho fescue, Parry oat grass, and smooth aster were obtained in late September of each year. The material was dried at 50°C and ten, 10-g samples of each species were prepared and placed into bags (10 × 20 cm) made of monofilament Pecap® polyester having a pore size of 51 ± 2 μm (B. & S.H. Thompson, Ville Mont-Royal, QC). These bags were placed under the litter layer, on top of the soil surface, in a rough fescue grassland site on 27 October in each year of the study. Two bags of each species were removed at monthly intervals until 15 April. The material was dried and weighed to determine biomass loss; the two subsamples were composited, ground in a UDY cyclone sample mill (UDY Corporation,

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Table 1. Effect of leaf position in the plant on the unit leaf weight and weight change after plant senescence in September and March for three tufted grass species over 3 yr. The means were estimated from 150 leaves taken from 30 plants for each species

Effect	Df	Parry oat grass		Idaho fescue		Rough fescue	
		Mean square (probability)					
Position (P)	4	0.068	(0.067)	0.008	(0.466)	0.214	(0.020)
P × Year (Y) (Error 1)	8	0.020		0.008		0.039	
Date (D)	1	0.508	(0.001)	0.007	(0.399)	0.117	(0.174)
P × D	4	0.007	(0.859)	0.007	(0.555)	0.092	(0.233)
P × D × Y (Error 2)	8	0.021		0.008		0.053	
		Means (mg)					
Position							
North		1.06*b*		0.55*a*		1.46*ab*	
East		1.00*ab*		0.53*a*		1.45*a*	
South		0.98*a*		0.54*a*		1.54*bc*	
West		0.97*a*		0.53*a*		1.52*bc*	
Center		0.99*a*		0.52*a*		1.60*c*	
Date							
September		1.04*b*		0.54*a*		1.54*a*	
March		0.97*a*		0.53*a*		1.50*a*	

a-c Means in column-subset having the same letter do not differ significantly ($P > 0.05$). Results were derived from paired comparisons using single degree of freedom contrasts.

Ft. Collins, CO), and analyzed for carbon and nitrogen by an automated combustion technique (Carlo Erba™, Milan, Italy).

Statistical Methods

The effect of leaf position within the plant on leaf weight and weight changes over time was tested using analysis of variance in a 5 (within-plant positions) × 2 (dates) × 3 (years) factorial design. The site effect was not significant ($P > 0.05$) and therefor the observations from each were pooled. Year was considered to be the random variable and its interaction with position used to test the main effect. All other effects were tested with the interaction of position × date × year. The dates represented herbage samples taken in August/September and March.

Changes in leaf biomass and chemical constituents were evaluated with the GLM procedure (SAS Institute, Inc. 1990) for analysis of covariance with species and year the main effects and the covariates representing days, from either 15 August to 27 March or 27 October to 15 April, and their quadratic. The model included the interactions of the main effects and their interactions with the covariates. The polynomial trends were over days and estimated by deriving the solution for the significant ($P < 0.05$) effects of the model. Where the trend was not significant ($P > 0.05$), only means were determined and tested for the effect of species and year using analysis of variance. Where a significant interaction existed for the main effects (year and species), the data were analyzed by year.

For the analyses of leaf biomass over days, average leaf weights per plant were determined as the unit of observation. The subsequent analyses resulted in a significant ($P < 0.05$) quadratic polynomial with a very small R^2 (<0.10) and an inflection that appeared to be an anomaly. Consequently, only the single degree polynomial was fitted to this data.

RESULTS

Standing Litter

1. Changes in biomass. The unit leaf weight was affected by position in the plants of Parry oat grass ($P = 0.067$) and rough fescue ($P = 0.020$); although leaf weight tended to decline over the period from September to March, position in the plant had no effect on biomass loss (Table 1). Leaf weights in Idaho fescue were not affected by position in the plant ($P = 0.466$).

From 15 August to 27 March, changes in unit leaf weight were similar ($P > 0.05$) among Parry oat grass, Idaho fescue, and rough fescue although their weights differed ($P < 0.05$, Table 2). According to statistical models (Table 2), estimates of proportionate losses by the end of March were 7, 18, and 13% for Parry oat grass, Idaho fescue, and rough fescue, respectively.

2. Nutritive constituents. The distribution of CP, P, and ADF over the period from 15 August to 27 March was expressed ($P < 0.05$) with second-degree polynomial equations (Tables 3 and 4, Fig. 1). During this period, the concentrations of CP and ADF were similar among grasses. Phosphorus concentration was greater for rough fescue than for Parry oat grass (Table 3). Smooth aster had a greater concentration of CP and P and a lower concentration of ADF than the grasses. However, ADF in smooth aster increased more rapidly over time and reached equality with the grasses before the end of March (Fig. 1). The trends over time were similar among years ($P > 0.05$).

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Table 2. Trends for leaf weight (mg cm^{-1}) after plant senescence from 15 August (X=day 0) to 27 March in important grass species over 3 yr on the fescue grasslands (models used in the development of the polynomial equations are given in the footnote[z])

	Intercept	X	R^2
Species[y]			
Parry oat grass	1.04*b*	–0.0003*a**	0.01
Idaho fescue	0.61*a*	–0.0005*a*	0.09
Rough fescue	1.62*c*	–0.0010*a*	0.04
SEest	0.03	0.0002	

[z]Whole model: effects (P, df): Species (<0.01, 2), Year (<0.01, 2), Day × S (<0.01, 3), D × Y (0.82, 2), D^2 × S (0.07, 2), D^2 × Y (0.17, 2), S × Y (0.92, 4), D (<0.01, 1), D^2 (<0.01, 1); R^2=0.76, df=609.
[y]Year effects were pooled to test species effects with 1st degree polynomials: (P, df) Species (<0.01, 3), Day × S (<0.01, 3); R^2 (error df)=0.75 (622).
a-c Means within a subset of column having the same letter do not differ significantly (P > 0.05).
* Denotes that the coefficient does not differ (P > 0.05) from 0.

Table 3. Trends for CP, P, and ADF after plant senescence from 15 August (X=day 0) to 31 March in important forage species on the fescue grasslands (statistics for selecting the terms of the polynomial models are given in Table 4)

Species	Intercept	X	X^2
Crude protein			
Parry oat grass	6.76*a*	–0.0374	0.00014
Idaho fescue	6.80*a*	–0.0374	0.00014
Rough fescue	6.89*a*	–0.0374	0.00014
Smooth aster	7.66*b*	–0.0374	0.00014
SEest	0.38	0.0078	0.00003
Grasses combined[z]	6.82*	–0.0374	0.00014
SEest	0.33	0.0077	0.00003
Phosphorus			
Parry oat grass	0.096*a*	–0.000638	0.00000220
Idaho fescue	0.103*ab*	–0.000638	0.00000220
Rough fescue	0.110*b*	–0.000638	0.00000220
Smooth aster	0.115*b*	–0.000638	0.00000220
SEest	0.007	0.000147	0.00000065
Grasses combined	0.103*	–0.000638	0.00000220
SEest	0.006	–0.000150	0.00000067
Acid detergent fibre			
Parry oat grass	40.2*b*	0.109*a*	–0.00040*a*
Idaho fescue	40.6*b*	0.104*ab*	–0.00036*a*
Rough fescue	40.0*b*	0.085*a*	-0.00028*a*
Smooth aster	23.9*a*	0.304*b*	-0.00096*b*
SEest	1.9		
Grasses combined	40.3*	0.099*	-0.00035*
SEest	1.0	0.023	0.00010

a,b Means in a column of a constituent having the same letter, or no letter, do not differ significantly (P > 0.05); all slopes are significantly different (P < 0.05) from 0.
[z]Consists of Parry oat grass, Idaho fescue, and rough fescue.
* Denotes that the means differ significantly (P < 0.05) from that of smooth aster.

The quadratic models describe increased concentrations of CP and P in late winter (Fig. 1). The slope may be an aberration of the model but, nevertheless, exists in the data for at least some groups. The average concentrations of CP near day 120 and day 200 (Fig. 1) were 4.71 and 5.13%, respectively, for the grasses but 5.94 and 4.99%, respectively, for smooth aster. However, only Parry oat grass had greater concentration of P at day 200 (0.60%) than at day 120 (0.55%).

Table 4. Analyses of covariance for the effects of species on CP, P, and ADF after plant senescence from 15 August (day 0) to 27 March (D = days as a covariate in the models shown in Table 3); years did not contribute significantly (P > 0.05) to the model and were pooled

Source	df	Crude protein	Phosphorus	Acid detergent fibre
			Probability	
Species (S)	3	0.11	<0.01	<0.01
S × Days (D)	3	0.46	0.07	0.04
S × D^2	3	0.58	0.22	0.20
D	1	<0.01	<0.01	<0.01
D^2	1	<0.01	<0.01	<0.01
Error	85			
			R^2	
		0.36	0.42	0.72

Buried Litter

The percent loss of biomass incubated under litter from 27 October to 15 April was similar among species (P > 0.05) but differed (P < 0.05) among years (Table 5). Estimated losses over 100 d were 7.1, 4.2, and 1.8% in 1992, 1993, and 1994, respectively.

The species effect on nitrogen concentration, nitrogen loss, and C:N ratio was different (P < 0.05) among years (Tables 5 and 6). Nitrogen concentration in smooth aster was greatest in 1993 and least in 1994. This corresponded to a net increase of nitrogen mass (indicated by a negative loss) and a lower C:N ratio in 1993 and a decrease in nitrogen mass and a greater C:N ratio in 1994 (Table 5). A species effect was not detected in 1992 for nitrogen concentration or C:N ratio (Table 5). The trends over time for concentration and mass of nitrogen, and the ratio of carbon to nitrogen, were significant (P < 0.05) only for rough fescue (Table 5).

The 1992/1993 study year was characterized by colder temperatures than the other 2 yr (Table 7) and snow cover that persisted to the end of March. Precipitation in 1993/1994 was similar to the previous year but warmer temperatures in December resulted in melting snow and generally reduced snow cover. Snow cover in 1994/1995 was almost absent due to low precipitation and snow melt during frequent warm periods.

DISCUSSION

Reduction in the concentration of nutrients in herbage was greatest in the late stages of plant senescence after 15 August (Fig. 1) and tended towards stability by December (day 120). Crude protein and P achieved minimum values by December and, apparently, increased in concentration toward the end of winter. Leaf biomass of standing litter decreased (P < 0.05) from August to March, the changes were small with no clear distinction between grass species despite their large differences in growth habit and leaf morphology. Idaho fescue is a small tufted plant while rough fescue is tall. Since these species grow within the same community, the taller plants are likely to shelter the shorter plants and, thereby, reduce exposure. The leaves of rough fescue are from three to five times as long as those of Idaho fescue or Parry oat grass while the latter is loosely tufted. The fescue species are “hard” grasses with a well-developed

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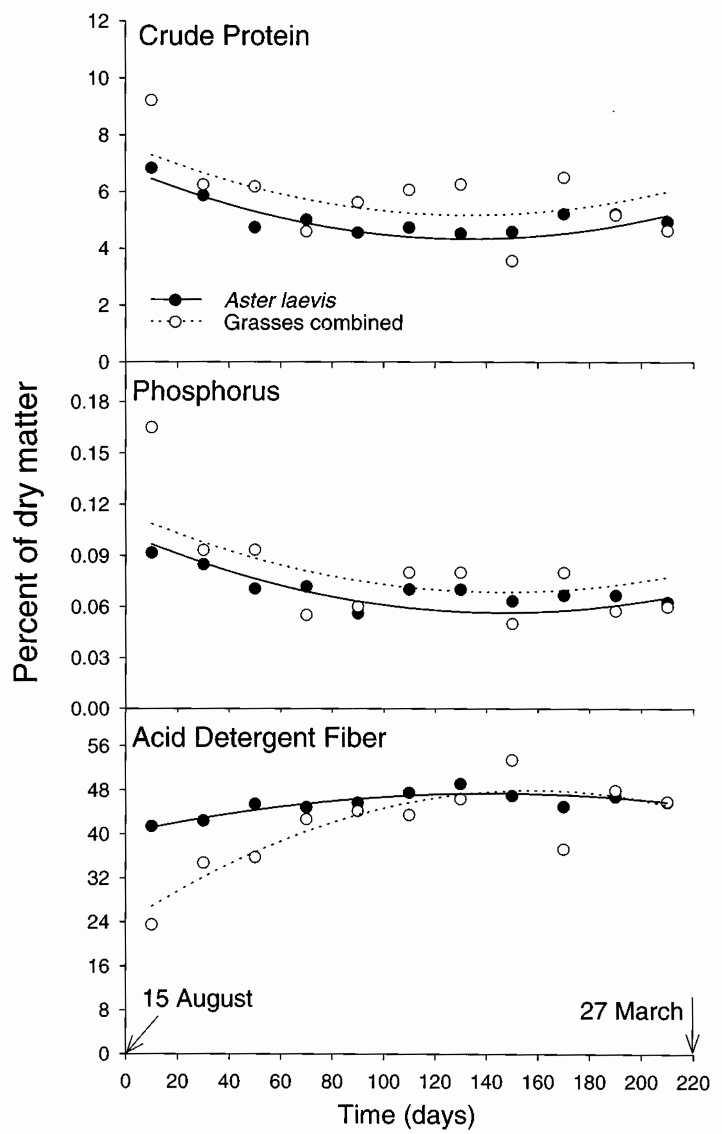

Fig. 1. Trends in CP, P, and ADF for *Aster laevis* and important grass species on the fescue grassland after plant senescence from 15 August to 27 March. Statistics and regression equations are given in Tables 3 and 4. The data points are the means for 20-d increments.

sclerenchymatous layer (Coupland and Brayshaw 1953) which may impair leaching or microbial decomposition while Parry oat grass has "soft" leaves. Lack of a detectable response to leaf weight among grass species may indicate that the largest changes had occurred prior to the start of the study, which represented the late senescence and weathering stage.

Weight changes in leaf biomass of standing litter over the fall and winter period were not affected by the contrasting temperature and precipitation conditions found among years (Table 7). However, buried litter seemed to be affected, having the greatest loss ($P < 0.05$) in 1992 (Table 5), a year with the greatest precipitation (Table 7), and the least in 1994 when precipitation was the least. Snow accumulation was also greatest in 1992, which was the result of persistent temperatures below freezing. Precipitation can increase losses due to leaching (Bleak 1970). Leaching and greater microbial decomposition might be expected under the more persistent snow cover which would insulate the canopy and increase the temperature of the leaf (Bleake 1970; Moorhead and Reynolds 1989).

Species had a relatively small effect on the rate of litter decomposition although there was a tendency for smooth aster to experience greater biomass loss ($P > 0.05$) than the grasses (Table 5). This might be expected because the leaves are more easily fragmented and, therefore, more susceptible to decomposition. Hunt (1977) and Vossbrinck et al. (1979) indicate that initial weight losses can be substantial and are caused by leaching of the labile mineral content.

The study yielded no evidence that leaf position in the plant affected exposure and biomass losses (Table 1). The prevailing winds are from the south-west and there is evidence that the weight of rough fescue leaves is greater on that side (Table 1). This may be a function of standing litter accumulating towards the north-east creating conditions that are less favourable for growth; a phenomenon that occurs

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Table 5. Trends of biomass loss, N concentration, change in N mass as a proportion of the original, and ratio of C to N in forage of important species when incubated under litter on the fescue grasslands from 27 October (day 0) to 15 April in each of 3 yr

	Biomass loss (%)		Nitrogen: Concentration (% of biomass)		Nitrogen: Loss of mass (% of original)	C:N	
	Intercept	*X*	Intercept	*X*	Mean	Intercept	*X*
Main effects							
Species[z]							
1992	0.495	0.068*c*	1.14	0.0006	1.1	39.7	–0.022
1993	0.495	0.047*b*	1.19	0.0003	–2.5	40.0	–0.022
1994	0.495	0.026*a*	0.80	0.0005	–3.4	59.0*b*	–0.022
Years							
Parry oat grass	–0.01	0.033*	0.92	0.0003	2.6	52.5	–0.016
Idaho fescue	0.07	0.033*	1.07	0.0003	–3.3	42.4	–0.016
Rough fescue	2.06	0.033*	1.12	0.0003	–2.6	40.0*a*	–0.016
Smooth aster	2.34	0.033*	1.03	0.0003	–3.6	52.7	–0.016
Species × Year							
1992							
Parry oat grass	–0.86	0.071	1.16*a*	0.0006NS	27.4*c*	40.3*a*	–0.022NS
Idaho fescue	–1.37	0.071	1.06*a*	0.0006NS	10.1*b*	41.8*a*	–0.022NS
Rough fescue	–0.24	0.071	1.12*a*	0.0006NS	–14.5*a*	39.3*a*	–0.022NS
Smooth aster	2.70	0.071	1.22*a*	0.0006NS	–13.7*a*	37.5*a*	–0.022NS
1993							
Parry oat grass	0.38	0.042	1.08*a*	0.0004NS	–2.5*ab*	42.6*b*	–0.018NS
Idaho fescue	0.16	0.042	1.05*a*	0.0004NS	–12.5*a*	43.9*b*	–0.018NS
Rough fescue	3.17	0.042	1.16*a*	0.0004NS	13.0*b*	39.7*b*	–0.018NS
Smooth aster	1.44	0.042	1.51*b*	0.0004NS	–20.3*a*	30.8*a*	–0.018NS
1994							
Parry oat grass	–0.76	0.018	0.62*a*	0.0006*	–12.5*a*	70.8*b*	–0.035*
Idaho fescue	–0.21	0.018	1.03*b*	0.0006*	–8.6*a*	44.0*a*	–0.035*
Rough fescue	0.37	0.018	1.00*b*	0.0006*	–13.6*a*	46.5*a*	–0.035*
Smooth aster	1.00	0.018	0.54*a*	0.0006*	9.0*b*	78.0*c*	–0.035*

[z]Treatment means were not tested where the year × species effects were significant ($P < 0.05$) (Table 6).
*Coefficients with an asterisk are different ($P < 0.05$) from 0; NS denotes that coefficients do not differ ($P > 0.05$) from 0.
a-c Intercepts, coefficients, or means within a subset of a column having the same letter, or no letter, do not differ significantly ($P > 0.05$).

Table 6. Analyses of covariance for the effects of species and year on biomass loss, N concentration, change in N mass as a proportion of the original, and ratio of C to N in forage when incubated under litter on the fescue grasslands from October to April (*D* = days as a covariate in the models shown in Table 5)

Source	df	Biomass loss (%)	Nitrogen: Concentration (% of biomass)	Nitrogen: Loss of mass (% of original)	C:N
		Probability			
Species (S)	3	0.56	0.47	0.34	<0.01
Year (Y)	2	0.48	<0.01	0.52	<0.01
S × Y	6	0.93	<0.01	0.14	<0.01
S × Days (D)	4	0.11	0.60	0.90	0.82
Y × D	2	<0.01	0.93	0.37	0.71
S × Y × D	6	0.19	0.08	0.09	0.29
D	1	<0.01	0.02	0.54	0.01
Error	65				
		R^2			
		0.84	0.84	0.70	0.89

[z]The analysis was repeated for individual years where the interaction of main effects was significant ($P < 0.05$).

when plants are ungrazed. However, biomass losses were, apparently, not affected.

Changes in the mineral and fibre (ADF) concentrations of grass leaves (Table 3, Fig. 1) are typical of the trends expected for the period of late senescence and weathering (Bezeau and Johnston 1962; Johnston and Bezeau 1962; Smoliak and Bezeau 1967). The changes in nutrients and biomass are interdependent since biomass loss is directly related to

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Table 7. Precipitation and average monthly temperatures during fall and winter of the study period over 3 yr in southwestern Alberta[z]

		Sep.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.
1992/1993	°C	10.2	6.2	–0.5	–10.6	–10.6	–7.2	1.2
	mm	42	37	44	25	8	18	30
1993/1994	°C	10.4	7.0	–3.0	–0.7	–6.0	–11.7	3.2
	mm	72	32	31	12	17	33	5
1994/1995	°C	14.3	6.2	–2.8	–4.0	–5.7	–3.2	–1.4
	mm	7	48	13	11	5	2	5

[z]Average from Pincher Creek and Claresholm (from Alberta Agriculture, Food, and Rural Development 1995; Alberta Agricultural Weather Summary, January to December, 1995. Vol. 9, Issue 35).

nitrogen concentration (Taylor et al. 1989). The trends followed closely the losses in biomass for the period with the exception that the concentration of nitrogen tended to increase towards the end of winter. Increases in nitrogen concentration were also observed in the litter component although the results were inconsistent among years and species (Tables 5 and 6). These inconsistencies may be explained by the availability of nitrogen since uptake by microbes is generally enhanced when useable carbon is abundant relative to nitrogen (Hunt 1977). Consequently, the nitrogen constituents tend to increase when the C:N is high and decrease when the ratio is low (Table 5).

Microbial decomposition associated with increased nitrogen after senescence may explain the observation by certain ranchers that grasses such as Altai wild rye (*Elymus angustus* Trin.), which seem unpalatable during the summer, become more acceptable to livestock in fall. Of course, an alternative explanation may be that the relative palatability of available forage species has changed as a result of senescence.

The grasses tested in this study could not account for the biomass losses of 53% or more observed on the fescue grassland community (Willms et al. 1996). This indicates that other plants, probably represented mostly by forbs, are more degradable and may disappear almost completely. Smooth aster, as a model of a forb, seemed to degrade more rapidly than grasses in the litter mass (Table 5) and is more susceptible to physical erosion when suspended on a stem. Loss of forb biomass was almost 60% compared with 27% for grasses (Willms et al. 1996).

Forage decomposition represents an important process that has significant implications for grazing and ecosystem functioning. We could not detect differences in the rates of decomposition of Parry oat grass, Idaho fescue, and rough fescue; and the forb, smooth aster, decomposed in a similar manner as the grasses for most parameters that were compared. Climatic conditions from one year to the next seemed to have the greatest effect on biomass and nutrient degradation particularly in the buried litter component. Decomposition reduces the amount and quality of herbage available for grazing and, thereby, reduces grazing efficiency. However, the consequence to the ecosystem may be positive if the nutrients are returned to the soil. On grassland soils where nitrogen is limiting, most leached nitrogen is immobilized by microbes and, therefore, contributes to the sustainability of the grassland ecosystem.

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