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Title: PHYSIOLOGICAL AND BIOCHEMICAL CHARACTERISTICS OF TWO CULTIVARS OF TALL FESCUE (FESTUCA ARUNDINACEA SCHREB.) UNDER DIFFERENT ENVIRONMENTAL CONDITIONS

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Dr. David O. Chilcote

Two cultivars of tall fescue (*Festuca arundinacea* Schreb.) with contrasting growth habits were studied under field and growth chamber conditions. Fawn, an established cultivar since 1964, and TFM, an experimental line, were observed to grow better during spring and fall months respectively, in the field. Different temperature regimes of 10/4, 16/4, 27/10, and 32/16°C were employed to study the effect of temperatures on the growth and biochemical characteristics of these two cultivars.

Fawn was significantly greater than TFM across the three harvests in dry matter production. There were no significant differences between Fawn and TFM in water-soluble carbohydrates (WSC) across the three harvest material. During the seven month period, there were also no

significant differences in water-soluble carbohydrates and crude protein between the two cultivars. Stems had a higher concentration of WSC but were lower in crude protein than leaves in both cultivars.

Fawn also produced more foliage dry matter (for the first and second harvests) across all temperatures tested. In regrowth, TFM and Fawn grew better at low and high temperatures respectively. This was expected on the basis of field results. Fawn was significantly greater than TFM in WSC and free sugars in both the first and second harvests and in the regrowth but in percent fructosans there were no significant differences between cultivars. TFM was significantly greater than Fawn in percent crude protein in both first and second harvest and regrowth. Temperature affected crude protein and WSC content as temperature increased, WSC, fructosan, and free sugars content decreased. Fructosans were lower in the regrowth material than either the first or second harvest. Percent crude protein in the foliage dry matter increased as temperature increased except in the regrowth where the lowest and highest temperatures showed the highest concentration.

Tillering was higher in Fawn, and the most favorable temperature for both cultivars was at 16/4°C.

Root dry weight was lower in Fawn, however, the concentration of WSC, fructosans, and free sugars in the roots were higher in Fawn than TFM. These sugar components were lower in the root material than in the foliage or regrowth material.

There were no differences in the mean relative growth rate between cultivars, although Fawn was highest at the high temperatures, with TFM being higher at the three lower temperatures.

There were no differences in net carbon exchange in the light or gross photosynthesis between these two cultivars, but Fawn was significantly greater in dark respiration at the highest temperature. Dark respiration and gross photosynthesis were higher at the highest temperatures in each cultivar.

TFM was significantly higher than Fawn in leaf area at the lower temperatures, but leaf area was lower at the highest temperature for both cultivars.

Fawn was significantly higher than TFM in perloline content across temperatures. In both cultivars, the higher temperatures had higher perloline content.

Physiological and Biochemical Characteristics of Two Cultivars of Tall Fescue (*Festuca arundinacea* Schreb.) under Different Environmental Conditions

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GENERAL INTRODUCTION

Tall fescue (Festuca arundinacea Schreb.) was introduced into the United States by early settlers from Europe for the use in addition to orchardgrass, timothy, red clover, and other forages. Tall fescue is a cool season, deep-rooted, long lived perennial. It is one of the best grasses available for poorly drained soils, and is widely used for forage, turf, and conservation purposes in the West, Northwest, and Southeast areas of the United States (21).

Fawn and TFM, two cultivars of tall fescue, differ in foliage growth as the season changes. Fawn tall fescue was developed by the Oregon Agricultural Experiment Station and has been commercially available since 1964. It is an 8-clone synthetic cultivar with good seedling vigor, spring growth and regrowth (39).

TFM tall fescue is an Oregon experimental line. It is a 12-clone synthetic that exhibits unusual cool season growth.

Because of the importance of tall fescue and the differing growth habits of these two cultivars, it was considered desirable to better understand the biochemical and physiological basis for the differences in growth and possible relationship of forage yield and quality.

The forage from both tall fescues, was analyzed for perloline content to examine the temperature effect on the level of this alkaloid in the harvest dry matter. Experiments were designed to examine these two cultivars in four different temperature regimes. The temperatures were employed to help describe the contrasting differences in growth. Dry matter water-soluble carbohydrates and crude protein content were determined for these two cultivars in each temperature. Net carbon exchange in the light and dark respiration was measured at each temperature to see if cultivars differed in photosynthetic activity.

GROWTH, DEVELOPMENT, AND CHEMICAL COMPOSITION OF TWO CONTRASTING CULTIVARS OF TALL FESCUE UNDER FIELD CONDITIONS

ABSTRACT

Forage yield, tillering, water soluble carbohydrates and total nitrogen were studied in two cultivars of tall fescue (*Festuca arundinacea* Schreb.), Fawn and TFM, in field conditions.

Fawn was significantly greater than TFM in dry matter production, averaging over three harvests during the growing season. TFM appeared to have more growth during the fall and winter months, but Fawn produced more dry matter than TFM based on the May 5th harvest date.

Tillering was greater for Fawn than TFM but greater weight per tiller was observed in TFM during April. In September, Fawn exhibited a greater weight per tiller.

Spring primordial development was more advanced in Fawn than in TFM. Regrowth recovery was faster for Fawn than TFM.

During a seven month period, Fawn and TFM were similar in both water-soluble carbohydrates (WSC) and crude protein content. Crude protein in the leaves was higher than in the stems for both cultivars. The reverse was true for WSC.

The highest accumulation of WSC in both stems and leaves for both cultivars occurred during the months of June and September. WSC concentration decreased after harvest and after nitrogen fertilizer application. The lowest levels of crude protein were observed during the month of June. Crude protein increased with the addition of nitrogen fertilizer and after each harvest.

There was a significant negative correlation between leaf crude protein and leaf water-soluble carbohydrates.

INTRODUCTION

Forage yield in grasses depends on their ability to both initiate and develop tillers, store carbohydrates, and nitrogenous reserves (77). Also, Ward and Blaser (93) have reported that the growth rate of orchardgrass depends on the sum of the responses of individual tillers.

Tillering contributes to the life of plants in two ways: (1) tillering of the young seedlings aids establishment, and (2) tillering is essential for the regeneration of the stand after harvesting (48), and for survival (4). Tillering and plant weight increase as defoliation decreased. This increase in tillering was attributed to more carbohydrates in the stubble bases where new tillers were formed (4).

The immediate reduction of assimilates after the removal of a substantial proportion of leaf area can cause a temporary reduction in the growth rate of the plant or sward (28). With no limiting factors, the most important determinant of regrowth is light energy converted to carbohydrates (28).

Carbohydrate reserves are used as substrates by perennial grasses for winter survival, early spring growth, regrowth initiation and respiration after herbage removal, before photosynthesis meets growth demands (76, 93, 97).

May and Davidson (57) and May (56), questioned the importance of carbohydrate reserves in controlling forage growth rate. They reported a decline of reserves after defoliation in subterranean clover, because of respiration rather than regrowth. They believe there is only indirect evidence supporting the role of carbohydrate reserves for regrowth.

Davidson and Milthorpe (32) stated that during the first two days following defoliation, carbohydrate reserves were not adequate for new growth and respiration. The contribution of protein and other labile fractions in the plant to new growth and respiration was four times those of carbohydrate reserves. They concluded (32) that carbohydrate reserves are part of the labile pool are are used for the synthesis of new compounds and respiration when photosynthesis is restricted, and that the size of the carbohydrate pool at defoliation could influence the regrowth. May (56) and Davidson and Milthorpe (33) believe that the decline in carbohydrate reserves after cutting is primarily due to use of carbohydrates in stubble and root respiration and not for regrowth. They concluded that the regrowth in Dactylis glomerata was dependent primarily on energy aided by photosynthesis from green parts of the stubble. However, Alberda (1) found that leaf growth occurs at the expense of the carbohydrate in the stubble since both the dry matter and the amount of carbohydrate in the regrowth decreases. Earlier work by Graber et al. (42) and Wiemman (96) support the hypothesis that herbage regrowth depends on the level of carbohydrate reserves.

Carbohydrate reserves are believed to decrease after cutting until sufficient leaf area is developed so that assimilates produced during photosynthesis can equal those used in respiration and regrowth (42, 90). Cridder (29) found that frequent and severe clipping generally reduced carbohydrate reserves and weakened the root system of grasses.

Blaser et al. (16) reported that it is very difficult to show the relative importance of leaf area and carbohydrate reserves since leaves not only photosynthesize but also have a significant carbohydrate content to add to the general pool of labile components.

Marshall and Sager (55) showed that carbohydrate compounds were transferred from the unclipped to clipped tillers within the plant only for the first few days following cutting. It appears according to Marshall and Sager (55) that the rate of regrowth depends both on carbohydrates and leaf area left in the stubble.

Nonstructural carbohydrates in early spring in fescue are primarily fructosans (53). Lechtenburg et al. (53) found that fructosan content did not vary in concentration during the growing period. This suggests that fructosans do not function as a leaf pool for temporary storage of photosynthates because of the lack of a diurnal trend. Fructosan functions more as a long term storage pool for carbohydrates in excess of those used in day-to-day growth and respiration.

The chief carbohydrate reserve found in cool season grasses is fructosan (93). Fructosan is a polysacharide with a β-2-6 linkage of fructose and terminating in glucose (71). Nonstructural carbohydrates (predominately fructosan) are temporarily stored in all parts of the plant, but the major storage region is believed to be the lower region of the stem bases (which include stolons, corms, and rhizomes) but not the roots (7, 76, 79, 85).

Protein is believed to be a labile substance which is used for respiration and new growth or roots and shoots in the first two to four days following a herbage removal (32). Dilz (36) found that in ryegrass proteinaceous compounds are important in regrowth and should be regarded as reserve contituents. It was also reported that the insoluble nitrogen compounds decreased sharply and soluble nitrogen compounds were used, but were not as important as carbohydrates reserved in support of regrowth.

Bidwell _et al_. (13) and Steward _et al_. (84) reported that nitrogenous sources account for 27 percent of the CO_2 released by respiration.

The objective of this study was to examine two cultivars of tall fescue with different seasonal growth habits for carbohydrates and crude protein levels, forage yield, tillering, and primordia development characteristics.

MATERIALS AND METHODS

Two cultivars of tall fescue (*Festuca arundinacea* Schreb.), Fawn, an established cultivar since 1964, and TFM (an experiment line), were planted June 24-25, 1974 at Hyslop Farm, Corvallis, Oregon, for forage evaluation. Each cultivar was planted in beds measuring 0.9 x 4.3 m with five rows per bed, in a randomized, complete block with four replications. Urea was used to supply nitrogen at 112 kg/ha, 70.9 kg/ha, and 89.6 kg/ha, on March 31, July 16, and September 24, respectively.

Three harvests were taken in 1975 for forage evaluation on May 8, July 11, and September 22. Forage yield was recorded as metric tons per hectare (m/ton/ha) of oven-dry matter. Tiller number for an area of 232.3 cm^2 was determined. Dry weight per plant was determined and the average of 20 plants was recorded. Plant height was also examined using six measurements per cultivar. Plant height and plant weight were taken on April 14 and September 2. Primordia development was observed on April 4, by dissecting 20 tillers of each cultivar.

Material from the three harvests was analyzed for water-soluble carbohydrates and crude protein. Also, samples were collected at intervals of 13 days for water-soluble carbohydrates (WSC) and every 26 days for total nitrogen determination over the period from 3/4/75 to 10/5/75. Each cultivar was sampled at random within each replication. Sampled material was immediately taken to the laboratory and microwaved for one minute to lessen respiratory losses during drying (101).

Leaves and stem material were separated. Stems were separated one inch above the first node. This material was dried at 70°C for 48 hours and then passed through a 40-mesh screen. The ground material was re-dried prior to WSC and total nitrogen analysis. WSC was extracted (Appendix II), and determined colorimetrically by the anthrone method of Yemm and Willis (104) with fructose as the standard. Total nitrogen was determined by the method of Nelson and Sommers (68) and reported as percent crude protein (%N x 6.25).

Primordia development, height of plants and weight per tiller data was not suitable for statistical analysis. The other characteristics examined were analyzed statistically.

RESULTS AND DISCUSSION

Forage Yield

Fawn was significantly greater than TFM in forage production when averaged across harvests. Data listed in Table 1 shows the levels of significance for harvest and cultivar means. Both cultivars produced more than twice as much forage on May 8 than on July 11 or September 22. These results show significant differences between cultivars for the July 11 and September 22 harvests, but not for the May 8 harvest. The rapid fall and winter growth of TFM versus the rapid spring growth of Fawn producing more forage, but the two cultivars did not differ in forage production on May 8. Due to a lack of nitrogen fertilizer and summer dormancy, the July 11 yields were low.

Tillering

Fawn had a greater number of tillers per 232.3 cm^2 (Table 2), 57.1 to 45.0 for Fawn and TFM, respectively. Carbohydrate accumulation determines tillering (4) and for the May 8 harvest, Fawn showed less water-soluble carbohydrates than TFM, perhaps because of its rapid growth rate (Fawn was usually higher in water-soluble carbohydrates). Eastin *et al*. (37) reported that during one rapid growth period soluble carbohydrates in bromegrass were at the lowest concentration. Fawn had smaller tillers (Table 2) than TFM in April so the higher tiller numbers of Fawn may have been due to less inter-tiller competition for light.

Plant Height and Weight

Plant height and weight per plant was greater for TFM than Fawn on the April 4 sampling date. TFM was 76.2 cm tall and weighed 1.41/g per tiller weight, whereas Fawn was 43.8 cm tall and weighed 0.76/g per tiller (Figure 1). This cultivar difference indicates that there are genetic differences for growth rate during the cool season of the year. Fawn showed greater plant height and tiller weight than did TFM on September 2. Fawn was 39.7 cm high and weighed 0.72 g/tiller whereas TFM was 29.8 cm high and weighed 0.429 g/tiller. Both cultivars decreased in plant height and plant weight during the summer months when compared to the spring growth, although Fawn appeared to grow better than TFM during the summer months (Table 2).

Both cultivars showed low water-soluble carbohydrate levels on September 22 (Table 4). This probably contributes to some of the poor growth due to lack of carbohydrate and higher respiration rates. Temperature and photoperiod probably affected the height and plant weight for each cultivar. Also, it was observed that during the summer months TFM displayed more narrow leaves in comparison

Table 1. Forage dry matter in metric tons/hectare[1/] for three harvests of two tall fescue cultivars, average of four replications, Corvallis, Oregon, 1975.

Cultivars	Harvests May 8	July 11	Sept. 22	Mean
Fawn	6.52	2.90	3.85	4.43
TFM	6.31	2.05	2.58	3.65
Mean	6.42	2.48	3.22	

[1/] $LSD_{.05}$ for cultivars = 0.057.
$LSD_{.05}$ for harvests = 0.200.
$LSD_{.05}$ for cultivars x harvests = 0.400.

Table 2. Tillering in (234.3 cm^2) plant height, and fresh wt/tiller of two cultivars of tall fescue sampled on two dates, Corvallis, Oregon, 1975.

Cultivars	No. of tillers[1,2/]	Date 4-14-75 Plant height (cm)	Date 4-14-75 Fresh wt/ tiller (g)[3/]	Date 9-2-75 Plant height (cm)	Date 9-2-75 Fresh wt/ tiller (g)[3/]
Fawn	57.1	43.8	0.76	39.7	0.723
TFM	45.0	76.2	1.41	29.8	0.419

[1/] Mean of four reps/232.3 cm^2.

[2/] $LSD_{.05}$ - N.S.

[3/] Mean of 20 tillers/cultivar.

Figure 1. The differences in growth in January between TFM and Fawn grown in field conditions. Blocks located from front to back; plots within blocks located from left to right. Fawn block 1 plot 2, TFM block 2 plot 4.

to Fawn, and this could explain part of the growth difference.

Floral Initiation

Primordial development was found to be different among these two cultivars. Fawn was more advanced during April than TFM, even though TFM was taller and appeared more advanced in growth. The height of the primorida in Fawn was 21.1 mm, but only 5.05 mm in TFM (Table 3). This represents the distance from the first node to the apex of the primordia.

Fawn was 100 percent reproductive while TFM was 75 percent reproductive and 25 percent vegetative (Table 3).

Water-Soluble Carbohydrates (WSC)

Fawn and TFM did not differ in WSC (mostly fructosans) across harvests (Table 4). However, significant differences occurred between harvests. The July 11 harvest was higher in WSC content perhaps due to less forage production (Table 1). Eastin *et al*. (37) also reported that in bromegrass, soluble sugar content was highest when growth was minimal.

Fawn accumulated 11.69 percent WSC on July 11 while TFM accumulated 10.19 percent WSC on May 8, which were the highest readings found among harvests. The lowest WSC levels for cultivars were for the September 22 harvest. TFM was significantly greater in WSC level on May 8, and slightly higher on September 22 than Fawn, possibly due to slower growth in TFM. Fawn may have utilized the substrates more rapidly than TFM because of an increased growth rate.

Crude Protein

There were no differences between cultivars in crude protein content across harvests. However, there were significant differences among harvest means. Significant differences occurred between cultivars on September 22 (Table 4). The September 22 harvest was higher in crude protein content than the May 8 or July 11 harvests, possibly due to the application of nitrogen fertilizer.

Yield, WSC, and Crude Protein Interrelationships

It was observed that as forage yield decreased (Table 1), percent WSC increased (Table 4), and percent crude protein decreased (Table 4) over harvests.

Fawn produced more forage dry matter during the summer months than TFM perhaps due to its ability to supply energy by photosynthesizing more assimilates. However, TFM had a more rapid growth rate during the fall months (Table 2), perhaps it needed less light energy to photosynthesize assimilates and to supply energy for maximum growth.

Figure 2 shows the cultivars having the same trend in crude protein content from harvest to harvest. The opposite in content between WSC and crude protein occurred in

Table 3. Primordia initiation and primordia length of two cultivars of tall fescue during April in field conditions.

Cultivars	No. of plants dissected	No. of plants/stage development	Average length of primordia (mm)[2]
Fawn	20	plants reproductive - 20	21.1
TFM	20	3 E.D.R.[1], 1 vegetative, 1 sterile, and 15 reproductive	5.05

[1] E.D.R. = Early double ridge.

[2] Length of primordia from first node to tip of the apex.

Table 4. Percent water-soluble carbohydrates and crude protein content in the forage content in the forage for three different harvests for two cultivars of tall fescue, Corvallis, Oregon, 1975.

	Harvests							
	May 8		July 11		September 22		Mean	
Cultivars	WSC[1]	Crude protein[2]	WSC	Crude protein	WSC	Crude protein	WSC	Crude protein
Fawn	7.65	7.54	11.69	6.38	4.96	8.93	8.10	7.61
TFM	10.19	7.64	8.94	6.16	6.94	7.44	8.69	7.08
Mean	8.92	7.59	10.32	6.27	5.95	8.18		

[1] $LSD_{.05}$ for cultivars - not significant.
$LSD_{.05}$ for harvests = 1.00.
$LSD_{.05}$ for cultivars x harvests = 2.00

[2] $LSD_{.05}$ for cultivars - not significant.
$LSD_{.05}$ for harvests = .5123.
$LSD_{.05}$ for cultivars = 1.020.

harvest dates. For Fawn, as WSC content increased, crude protein decreased. TFM did not show this same relationship (Figure 2). TFM declined in WSC content from May 8 to the September 22 harvest, whereas crude protein declined from May 8 to July 11 then increased for the September harvest (Figure 2).

The Fluctuation of WSC and Crude Protein Content during a Seven Month Growing Period

Water Soluble Carbohydrates (WSC)

WSC concentration (mostly fructosans) decreased in both stem and leaf tissue with each harvest date. Alberda (2) reported a decrease in water-soluble carbohydrates after clipping. Stems were higher in WSC content than leaves (Tables 5, 6). No differences in WSC between cultivars in either stem or leaf tissue occurred across samples taken over a seven month period. There were significant differences in WSC between sampling dates in leaves and stems. A significant cultivar x sampling date interaction occurred for leaves but not for the stems. Table 5 shows June and September stem WSC content higher than the other sample dates. The lowest WSC content was observed during May and October, two weeks after harvesting. On August 20, September 2 and 15, TFM was significantly greater in stem WSC than Fawn while Fawn was significantly higher on sampling dates of May 8, 21; June 3, 29; and October 5. Fawn's

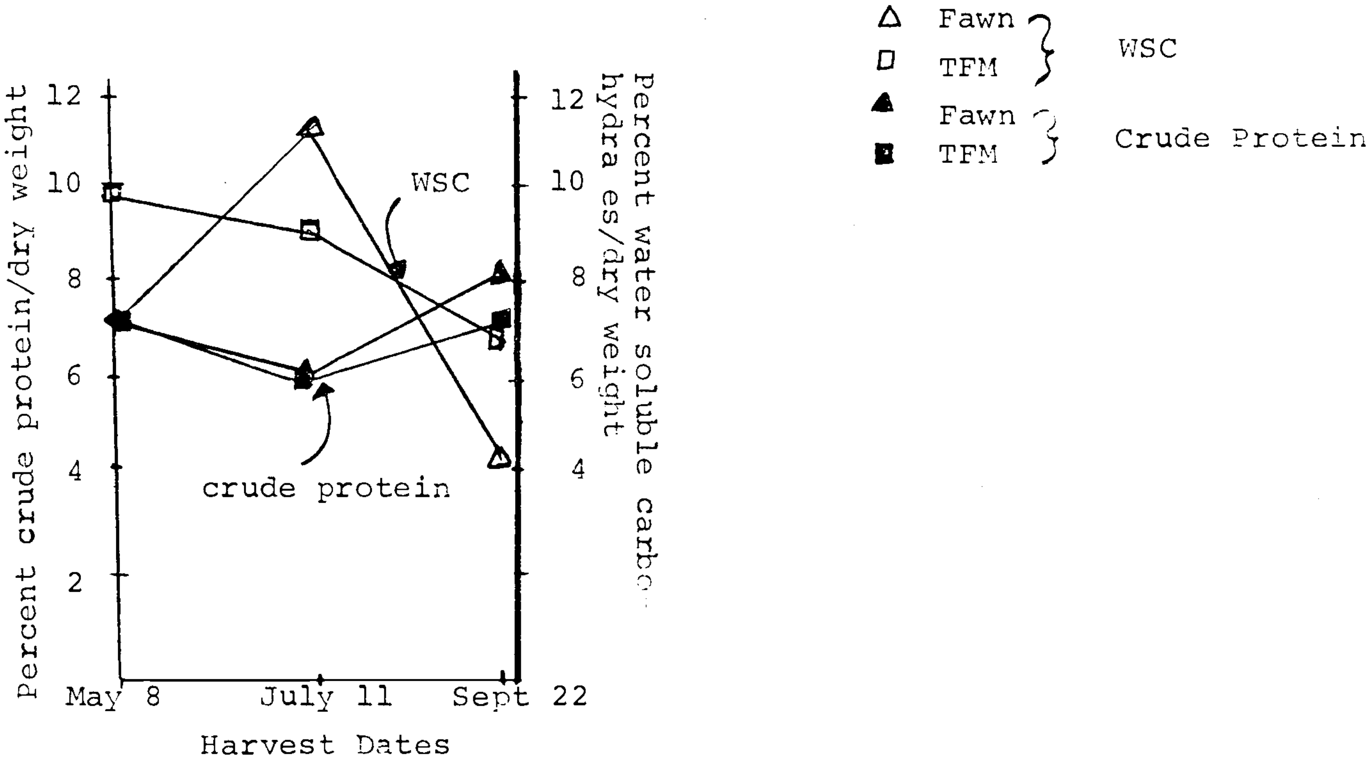

Figure 2. The percent of WSC and crude protein taken at three different forage harvests for two cultivars of tall fescue grown in field conditions.

highest accumulation of stem WSC was in June, where TFM's highest accumulation was in September (Table 5).

Fawn and TFM leaves accumulated more WSC content in June, while the lowest accumulation in WSC occurred on October 5, July 25, and August 7 for both cultivars. The highest WSC accumulation, across cultivars, occurred in June, apparently due to reduced forage growth.

Some of the fluctuation in WSC content of stems and leaves across the season might be explained on the basis of diurnal variation in WSC (Figure 3). Holat and Hilst (45) reported that soluble-sugars in tall fescue increased from six percent at 6 AM to nine percent at 6 PM. Stored non-structured carbohydrates are more stable than labile soluble-sugars but some diurnal variation in non-structural carbohydrates might occur. WSC concentration in leaves and stems had the same trend in both cultivars during the growing season (Figure 3).

Crude Protein Content

No differences in crude protein content in leaves or stems occurred between cultivars. However, significant differences existed in sampling dates in both leaves and stems (Tables 5 and 6).

Sampling dates were all significantly different from each other in leaf and stem crude protein, except on May 8, where stem tissue did not differ from the May 21 date.

Table 5. Seasonal variation of water-soluble carbohydrates and crude protein levels in the stems of two cultivars of tall fescue sampled during the growing season, Corvallis, Oregon, 1975.

	Percent WSC[2]			Percent Crude protein[3]		
	Cultivars			Cultivars		
Dates	Fawn	TFM	Mean	Fawn	TFM	Mean
4-14	20.10	21.32	20.66	----	----	----
5-8	21.32	18.77	20.04	3.23	3.75	3.49
5-21	12.52	8.49	10.41	----	----	----
6-3	18.75	14.68	16.71	3.52	3.64	3.58
6-16	24.93	23.97	24.45	----	----	----
6-29*	26.51	24.49	25.50	2.88	2.83	2.85
7-25	13.70	12.55	13.12	----	----	----
8-7	16.22	17.11	16.67	7.06	6.04	6.55
8-20	20.85	23.37	22.11	----	----	----
9-2	22.44	25.14	23.79	5.62	4.42	5.02
9-15*	22.84	24.15	23.50	----	----	----
10-5	12.99	9.97	11.48	8.89	9.45	9.17
Mean	19.43	18.66	Mean	5.20	5.02	

[1] Mean of four replications

[2] Sampled at 13-day intervals, except at * due to forage harvest.

[3] Sampled at 26-day intervals, except at * due to forage harvest.

$LSD_{.05}$ for cultivars = not significant
$LSD_{.05}$ for samples = 1.07.
$LSD_{.05}$ for cultivars x sample = 2.15.

$LSD_{.05}$ for cultivars = not significant.
$LSD_{.05}$ for samples = .56
$LSD_{.05}$ for cultivars x sample = 1.11.

Table 6. The seasonal variation of water-soluble carbohydrates and crude protein levels[1] in leaves of two cultivars of tall fescue sampled during the growing season, Corvallis, Oregon, 1975.

	Percent WSC[2]			Percent Crude protein[3]		
	Cultivars			Cultivars		
Dates	Fawn	TFM	Mean	Fawn	TFM	Mean
4-14	6.60	6.71	6.65	-----	-----	-----
5-8	9.50	8.90	9.20	10.15	11.23	10.69
5-21	8.30	5.55	6.92	-----	-----	-----
6-3	11.75	10.18	10.96	8.46	9.44	8.95
6-16	13.36	17.21	15.29	-----	-----	-----
6-29*	18.81	14.98	16.90	6.16	6.80	6.49
7-25	2.59	2.31	2.45	-----	-----	-----
8-7	5.24	3.77	4.50	14.82	16.01	15.42
8-20	6.18	5.84	6.00	-----	-----	-----
9-2	7.52	9.75	8.64	10.22	11.73	10.98
9-15*	6.70	10.37	8.79	-----	-----	-----
10-5	3.44	2.18	2.81	19.98	16.69	18.33
Mean	8.33	8.19		11.63	11.98	

[1]Mean of four replications.

[2]Sampled at 13-day intervals, except at * due to forage harvest.

[3]Sampled at 26-day intervals.

LSD$_{.05}$ for cultivars = not significant
LSD$_{.05}$ for samples = 0.78
LSD$_{.05}$ for cultivars x sample = 1.56.

LSD$_{.05}$ for cultivars = not significant.
LSD$_{.05}$ for samples = .74
LSD$_{.05}$ for cultivars x sample = 1.56.

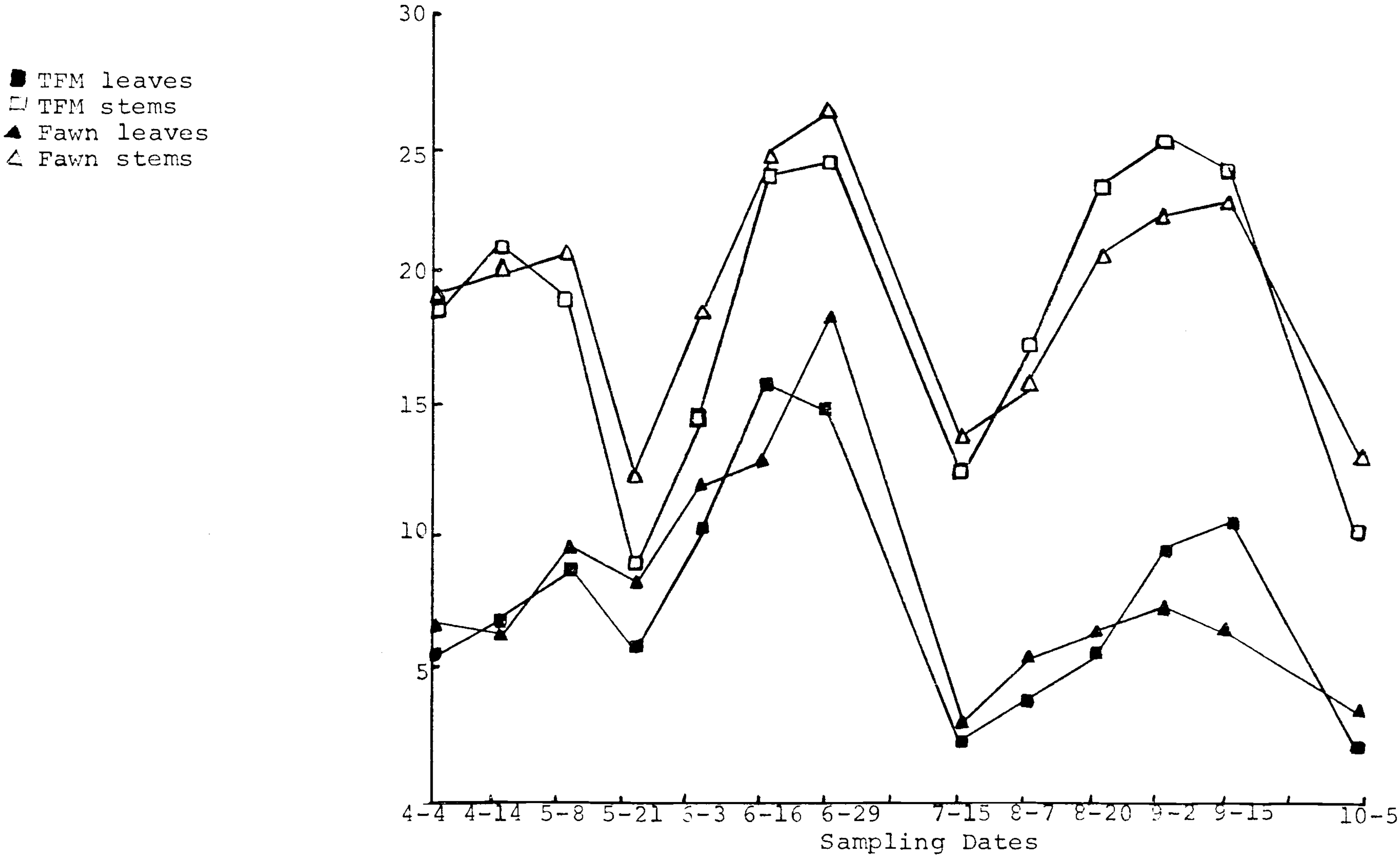

Figure 3. Changes in percent water-soluble carbohydrates in leaves and stems over a seven month period for two cultivars of tall fescue grown under field conditions, Corvallis, Oregon, 1975.

Leaves were higher in crude protein than stems in both cultivars (Figure 4), probably due to more chloroplasts and perhaps less fiber content in the stems. Fifty percent of the chloroplast weight is believed to be protein. Leaves were lower in crude protein content on June 29, while the highest concentration occurred on October 5 because of the application of nitrogen. On October 5, crude leaf protein was 19.98 and 16.69 percent for Fawn and TFM respectively, and the stem protein was 8.80 and 9.45 percent for Fawn and TFM respectively. Crude protein content in leaves and stems had the same trend in both cultivars during the growing season (Figure 4).

Carbohydrates and Crude Protein Interaction

A significant negative correlation between WSC and crude protein was found in stems and leaves (average in cultivars) across the seven month season (Figures 5 and 6). As WSC increased, crude protein decreased in both stems and leaves. Competition for carbon skeletons might be responsible for the negative association between crude protein and WSC. Prianisknikov (72) explained that carbon skeletons for protein (via amino acids) are supplied by carbohydrates.

Leaves were higher in crude protein and lower in WSC, while stems are lower in protein and higher in WSC (Tables 5 and 6). The levels of WSC and crude protein in the stems for the October sample were similar in TFM, but Fawn had

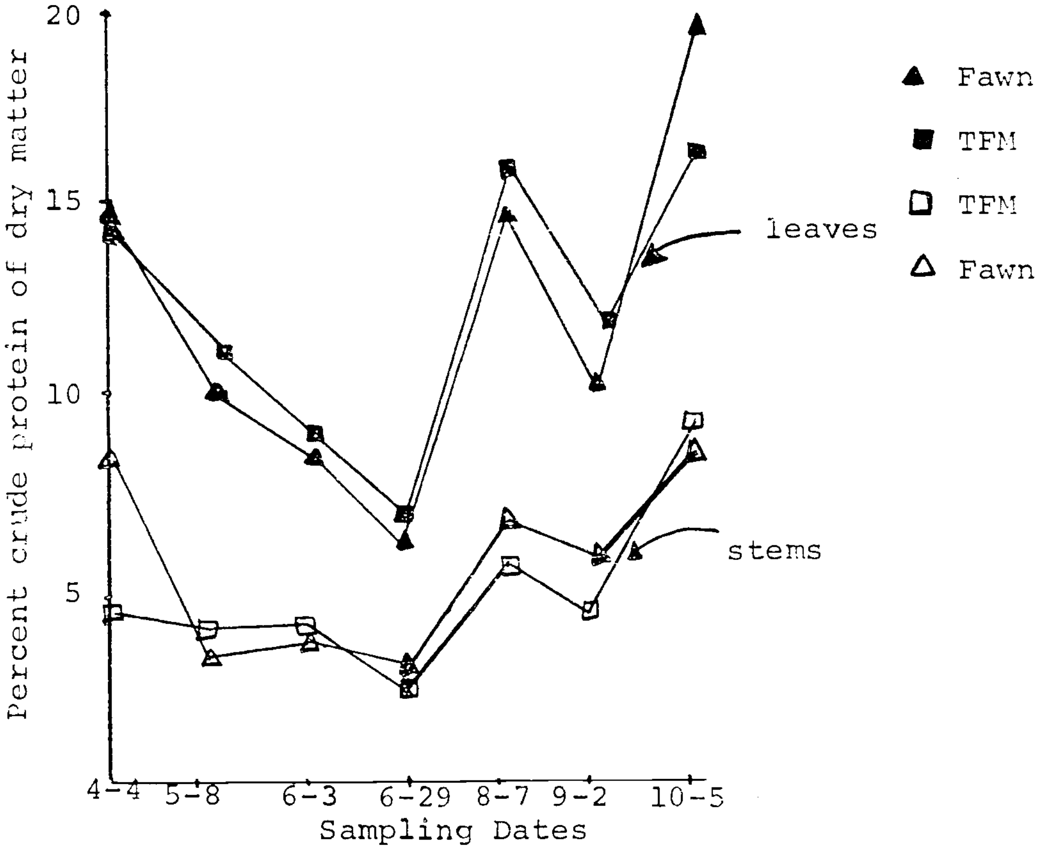

Figure 4. Crude protein in leaves and stems for two cultivars of tall fescue under field conditions, Corvallis, Oregon, 1975.

12.97 percent and 8.89 percent for WSC and crude protein, respectively (Figure 5). The June sample had the highest WSC content of all the samples, with 26.51 and 24.49 percent for Fawn and TFM respectively. Crude protein content was lowest on June 29 with 2.88 percent for Fawn and 2.85 percent for TFM.

WSC and crude protein content for Fawn leaves were highest for the June 29 and the October sample respectively with 18.81 and 19.98 percent. The lowest levels of WSC and protein in Fawn leaves were on the October and June 29 samples with 3.44 and 6.16 percent, respectively.

TFM was highest and lowest in the same two months as Fawn for WSC and crude protein content in leaves. TFM had the highest WSC and crude protein content on June 29 with 14.98 and 16.69 percent, respectively (Figure 6). The lowest concentration on WSC and crude protein occurred in the October and on the June 29 samples with 2.18 and 6.80 percent, respectively. This agrees with Sosebee and Wiebe (87) who reported that the level of carbohydrates were highest during the mid-summer due to dryer and warmer weather, which resulted in an internal moisture deficit that decreased carbohydrate utilization by slowing transportation. Crude protein was lower in June due to matured plant parts and older leaves. According to McKee (59), protein synthesis is active only in young leaves and soluble nitrogenous substances produced are translocated

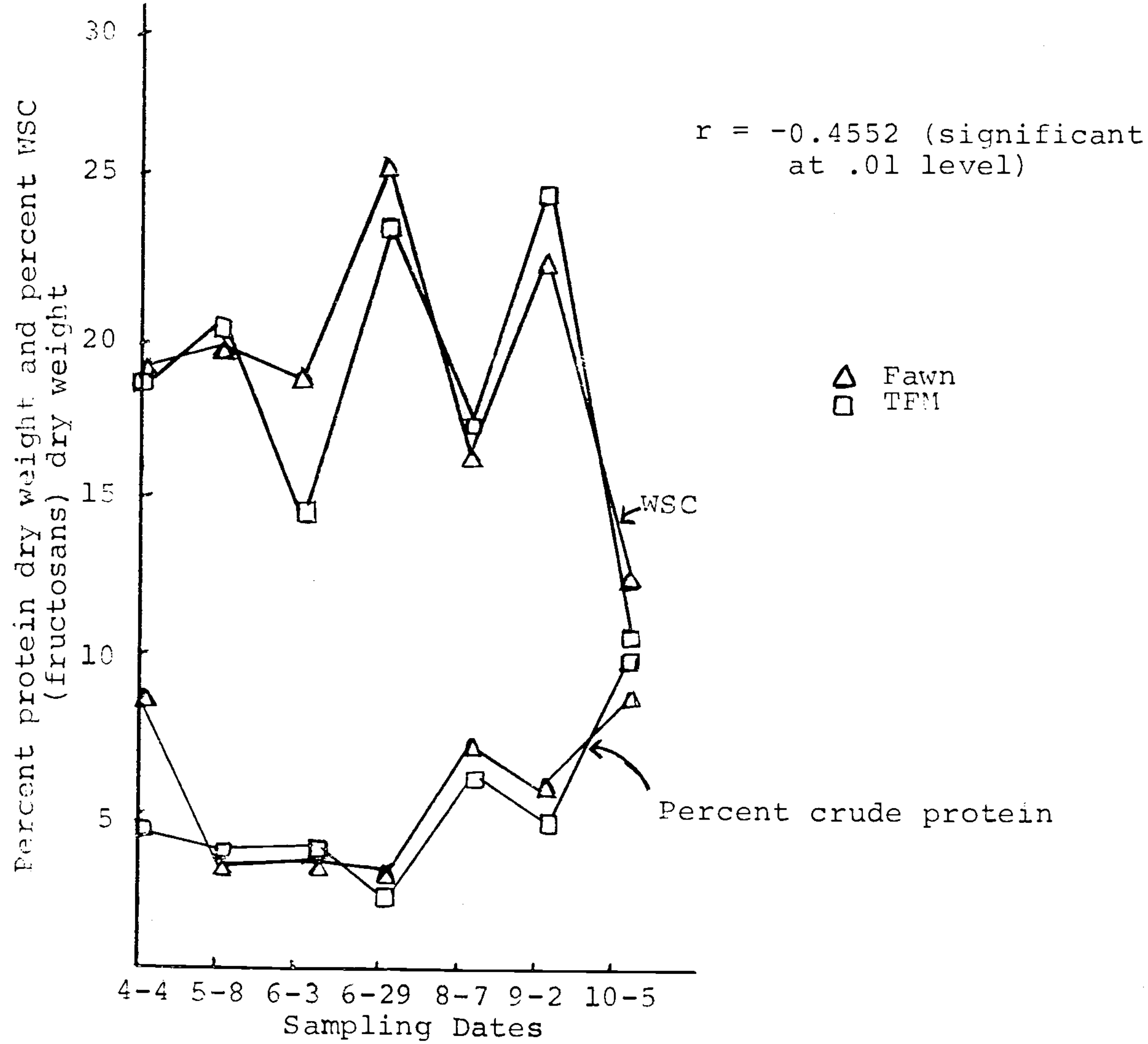

Figure 5. Seasonal variation of crude protein and water-soluble carbohydrates in stems for two cultivars of tall fescue grown under field conditions, Corvallis, Oregon, 1975.

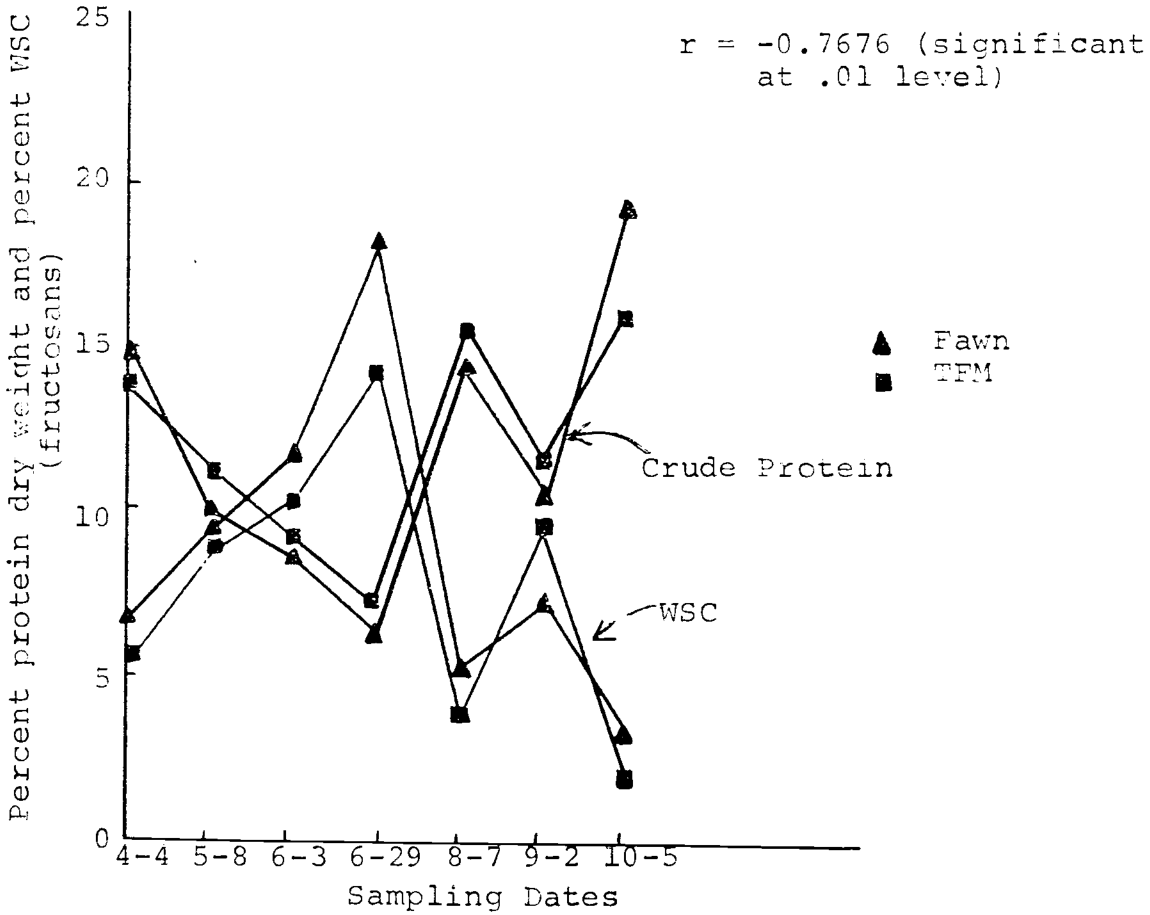

Figure 6. Variation in crude protein and water-soluble carbohydrates in leaves for two cultivars of tall fescue grown under field conditions, Corvallis, Oregon, 1975.

to other sites of protein synthesis. As the plant matured, nitrogen content in the plant material decreased.

Nitrogen application increased protein content (23) and decreased carbohydrate content (20, 53).

Conclusions

Fawn was significantly greater in forage production across harvests. The number of tillers was greater for Fawn. Plant height and tiller weight was greater for TFM in April, but Fawn was greater in September. In April, primordia development was more advanced in Fawn. There were no cultivar differences in WSC and crude protein across harvests or in frequent samples during the seven month study. Significant differences had occurred in WSC and crude protein among forage harvests and the frequent sampling dates. The highest accumulation of WSC and lowest accumulation of crude protein content for both cultivars was the June 29 sample. This was attributed to reduced growth during June.

A negative correlation between protein and WSC occurred in both leaves and stems.

THE EFFECT OF TEMPERATURE ON THE MORPHOLOGY AND CHEMICAL CHARACTERISTICS OF TWO CULTIVARS OF TALL FESCUE GROWN UNDER CONTROLLED ENVIRONMENTAL CONDITIONS

ABSTRACT

The effect of four temperature regimes on root, growth, dry matter production (sum of first and second harvests), regrowth, tillering, and chemical components were examined in two contrasting cultivars of tall fescue (Festuca arundinacea Schreb.), i.e., Fawn, an established cultivar and TFM, an experimental cultivar showing winter growth habit.

Fawn was significantly greater than TFM in dry matter production across harvests and temperatures. Fawn produced more dry matter at the first and second harvests than did TFM. Both cultivars produced more dry matter at the two higher temperatures.

Fawn was significantly higher in tillering than TFM across temperatures and harvests.

Water-soluble carbohydrates (WSC), which consisted of fructosans and free sugars were higher in concentration at the lower temperatures. Both fructosan and free sugar content was lower at the highest temperatures.

TFM was significantly greater than Fawn in crude protein content across temperatures and across harvests.

Regrowth dry matter production in Fawn and TFM was different depending on the temperature regime. Fawn produced more regrowth at the warmer temperatures (32/16 and 27/10 °C), while TFM produced more at lower temperatures (10/4 and 16/4°C). These results were expected based on field observations.

WSC content was higher at the lower temperatures. WSC was slightly lower in regrowth than in previous harvest material.

Crude protein was higher in TFM than Fawn in the regrowth dry matter. The higher content of crude protein was at 10/4 and 32/16°C and lower at 27/10 and 16/4°C for both cultivars.

There were no differences in mean relative growth rate ($\overline{RGR}$) between cultivars, although TFM tended to be higher in $\overline{RGR}$ at the lowest temperatures and Fawn higher at the higher temperatures.

TFM was slightly higher in root dry weight, but Fawn had a longer root system. Root dry weight was higher at the higher temperature regimes.

WSC content in root dry matter was very low at all temperatures in comparison to top growth dry matter (first and second harvests, and regrowth dry matter).

Fawn was higher in root fructosans than TFM.

Fructosan levels were higher than free sugars at the lowest temperature across the first and second harvest dry matter material. However, the percent free sugar was higher than percent fructosan in the regrowth dry matter.

INTRODUCTION

Tall fescue (Festuca arundinacea Schreb.) is one of the most widely grown cool-season forage grasses in the upper south and Pacific Northwest (87). Some genotypes exhibit dramatically different growth habits.

In Western Oregon, Blacklow (15), found that cultivars from the Mediterranean region produced more foliar growth during the winter, but less during the summer, than the Northern European cultivars. He concluded that seasonal growth could be interpreted as ecotypic variation, enabling species to survive seasons of stress in the regions of origin.

Growth and morphology of seedlings of tall fescue have been shown to be affected by temperature. According to Kendall (50) and Mitchell (63), every plant species has an optimum temperature for growth.

Robson and Jewiss (73, 74) observed that SYN II, a North African synthetic, produced more dry matter under cool temperatures than S 170, a British genotype. The growth differences observed at 5.8/05°C for day/night between these two cultivars disappeared when the temperature increased to 11.7/1.5°C, day/night regimes.

Youngner and Nudge (103) found top growth production in bluegrass to be greater at temperatures of 21/27 and 16/27 than at 18/13 and 16/7°C night/day, respectively.

Growth rate, yield, tillering, leaf blade area, and specific leaf blade weight were higher in timothy, cocksfoot and tall fescue at a temperature of 18/10 compared to 32/24°C (51).

Temperature regimes of 25/12, compared to 25/25 or 12/12°C, produced more dry matter for both Italian and Irish perennial ryegrass (11).

Beevers and Cooper (11, 12) reported that different temperature regimes changed vegetative morphology of ryegrass, due to metabolic activity at the cellular level associated with changes in chemical constituents.

The effect of temperature on the percentage of carbohydrate reserves in the stem bases is influenced by the origin of the grass species (97).

Beevers and Cooper (12) found that dry matter of ryegrass growing continuously at 12/12°C had higher carbohydrate levels than when growing at 25/12 or 25/25°C day/night temperature regimes.

At low temperatures, water soluble sugars accumulate in cultivars which have poor growth rate at time of clipping (73, 103). Brown and Blaser (20) reported that high temperatures during July and August apparently did not keep the reserve carbohydrate at a low level. They concluded that high temperatures may influence reserve carbohydrates through the effect on growth and metabolism, but under the conditions of drought and in mature plants, high temperature may be relegated to a secondary role.

High accumulation of carbohydrates in cool temperature regimes suggest that slow growth of plants at low temperatures is not due totally to shortage of photosynthates (12). Temperature appears to influence the accumulation of fructosan (80). Fructose is the main nonstructural sugar of temperate-origin grasses. Sullivan and Sprague (86) found that fructosans in the stubble decreased to a low percentage under high temperature regimes and remained low for the 40-day regrowth period. But at lower temperature regimes, fructosans were higher and eventually were restored to near their original concentration.

Waite (91) concluded that fructosans account for much less of the total water-soluble carbohydrates in warm climates than in cold regimes, which suggests that at higher temperatures there are less fructosans to be affected.

There are differences in the effects of high night temperatures as opposed to high day temperatures according to Baker and Jung (6). They point out that high night temperatures decrease carbohydrate reserves of temperate-origin grasses, more than high day temperatures. They concluded that increasing the day temperature, if below optimum, increases both respiration and photosynthesis; whereas increasing the night temperature increases only the respiration rate, and thereby decreases the reserve level.

Smith and Jewiss (81) suggested that during high night and day temperatures, the percentage of water-soluble carbohydrates in the stems of timothy decreased.

Temperature has also been shown to affect the total nitrogen content in grasses (12). Total nitrogen content was greatest at 12/12°C, decreased at 25/12 and was lowest at 25/25°C. These results are similar to those of Bathurst and Mitchell (8).

Beevers and Cooper (12) believed the reason cool temperature regimes had higher total nitrogen is that these plant leaves mature slowly, with less rapid hydrolysis of protein and slow translocation of nitrogen occurring from these leaves at the lowest temperature.

Productivity and survival of perennial grasses depends on the lifespan and physiological responses of individual tillers to various environmental factors (4).

Differences in tillering of tall fescue at several locations was believed, according to Youngner and Nudge (103), to be due to temperature. Increasing night temperature from 10 to 15 to 25°C decreased tiller number in ryegrass. Tillering in tall fescue has been shown to be increased by low temperatures (62, 87). Buckner _et al_. (22), reported that tall fescue tillered more at 6.8°C than at 13.9°C. Nittler _et al_. (69) concluded that temperature did not cause much difference in total tiller production in varieties of orchardgrass.

Regrowth of perennial grasses is positively associated with rapid tillering, carbohydrate content and the remaining leaf area of the stubble (18, 93). Carbohydrate reserves stimulate new tiller development, and are more important to tillering than leaf area during the first 25 days of regrowth (93). High temperatures decrease carbohydrate reserves in cool season grasses which also effect the regrowth (11, 12, 19, 86).

Graber *et al.* (42) found that nitrogenous compounds are important for regrowth determination and root growth, but carbohydrates are believed to be more essential than nitrogen compounds in supplying stored energy for regrowth. There was a negative correlation between protein and carbohydrate content in regrowth (72). He concluded that this might be due to carbon skeletons from carbohydrate reserves being used in formation of aminoacids to proteins.

The association between Relative Growth Rate (RGR) and temperature changes with plant age. Milthorpe (61) and Thorne (88) have recorded a decrease in RGR as plants age in warm environments, due to an increase in self-shading and the increased ratio of respiring to photosynthetic tissue. Also, Beevers and Cooper (11) found that differences in RGR in ryegrass were due to temperature regime and plant age. They concluded that the lowest RGR was observed at 12/12 followed by 25/25 and the highest was shown at 25/12 because of a greater LAR and a 12/12°C was lowest because of early stages of growth. Although plants grown at 12/12°C regime produced leaves less rapidly than at 25/12 or 25/25°C, the leaves were heavier per unit area basis and were larger in area.

Beevers and Cooper (11) found that at lower temperatures roots have an advantage and root/shoot ratio increases. Root dry weights were found to be lower at 12/12 and highest at 25/12°C.

Smith (80) found that roots of plants grown under warm temperatures contained very small amounts of fructosan, while those grown under cool conditions produced considerable amounts of fructosan.

Carbohydrates are found in less quantities in roots than stems or leaves and Marshall and Sagar (55) concluded that carbohydrates in the roots were not mobilized to the shoots for support of regrowth.

Experiments were conducted to study the effects of temperature on two cultivars of tall fescue which exhibit contrasting growth habits. Fawn, an established tall fescue cultivar since 1964, is a very good forage and seed producer in the Willamette Valley (39) throughout the season, but does not yield as well as TFM, an experimental line, during the fall months.

The influence of temperature on the first and second harvest dry matter production, regrowth, tillering, carbohydrate, and protein content was evaluated under controlled environments with four different temperature regimes.

MATERIALS AND METHODS

Seeds of two cultivars of tall fescue, Fawn and TFM, were planted in flats containing vermiculite and germinated at 21/10°C. After germination, the flats were placed at 27/10°C for faster growth. After one month, three plants were transplanted into 10 cm pots in a soil of two parts sand to one part peat soil.

Pots were thinned to two plants each. Plants were grown an additional month in the greenhouse at 25/12°C, then clipped to 5 cm and placed in controlled environments at the respective temperature. Day/night temperature regimes of 10/4, 16/4, 27/10 and 32/16°C ± 1°C were used with photoperiods of 11.5 and 12.5 hours, day and night respectively. Light intensity ranged from 1300 to 1800 ft.c. per chamber supplied by incandescent and fluorescent lights. Two harvests and regrowth measurements were taken on the two cultivars of tall fescue. A completely randomized design, with ten observations (pots) per treatment, was used. A complete nutrient solution was applied until a maximum of 144 kg/ha of nitrogen was added (54).

Foliage Dry Matter

The first and second harvests occurred at 22 and 44 days, respectively, after placement in the appropriate growing temperatures. The ten pots in each treatment were pooled to form five observations. This allowed enough material for chemical analysis.

Clippings of the first and second harvests were dried at 70°C for 48 hours before weighing. After weighing, the oven-dried material was ground to pass through a 40-mesh screen. Ground material from the first or second harvest was kept in metal containers and re-dried before water soluble carbohydrates and total nitrogen were analyzed.

Regrowth

Those plants from the first and second harvest were kept for regrowth analysis, and 13 days after the second harvest, regrowth from both harvests were taken (13 and 35 days after the original harvest), dried, ground, and stored as previously described. Water-soluble carbohydrates and total nitrogen were analyzed. Only eight observations, or pots, of the ten observations were used in the regrowth study, the two other observations were left for further testing. Those eight observations were added to make four observations (two pots) per treatment. Dry weight, water-soluble carbohydrates and crude protein were determined and recorded.

Tillers were counted before the pots were placed in each temperature and after each harvest. Again, ten observations were pooled to make five observations per treatment.

The mean relative growth rate ($\overline{RGR}$) was calculated on the basis of ten observations per treatment. The formula used to calculate $\overline{RGR}$ was:

$$\overline{RGR} = \frac{\ell_n W_2 - \ell_n W_1}{t_1 - t_2} \quad (15,100)$$

The initial and final weight of plant material was represented by W_1 and W_2, respectively, over the time interval $t_2 - t_1$ (22 days).

Roots were removed from the soil at the end of the experiment, washed, oven-dried, weighed and ground as previously stated (refer to foliage dry matter). Water-soluble (WSC) carbohydrates were extracted from the roots. Four observations for dry weight and WSC per treatment were used.

Water-soluble carbohydrates were extracted first using 90 percent ethanol for free sugar and then using water for extracting fructosans (Appendix II). Water-soluble carbohydrates are the summation of fructosan and free sugar.

Yemm and Willis (104) anthrone method using the spectrophotometer to determine concentrations of water-soluble sugar was used. Fructose was used as a standard.

Total nitrogen was determined after Nelson and Sommers (68) and expressed as percent crude protein by a conversion factor (Total N x 6.25).

RESULTS AND DISCUSSION

Dry Matter Production

Fawn produced more dry matter for the first and second harvests than TFM across temperatures. The lowest accumulation of dry matter for both cultivars occurred at temperatures of 10/4, followed by 16/4 and 32/16°C. The most favorable temperature for TFM in both harvests was 27/10°C and Fawn had its greatest production at 32/16°C (Table 7). The results were as expected for Fawn, with higher yields at the higher temperatures, but not for TFM. It was noticed in field observations that TFM tends to grow better at fall temperatures, however, this was not found, probably due to insufficient time at these temperatures for this expression of growth habits. There were differences in dry matter production between temperatures (Table 7). Fawn's yield was significantly greater than TFM's at every temperature in each harvest, except at 27/10°C.

Tillering

Tillering was significantly greater at the second harvest than the first harvest because of the longer time for development. Tillers from the first harvest (22 days of growth) were almost equal for Fawn and TFM, but during

Table 7. The effect of temperature on dry matter[1/] of two cultivars of tall fescue at two different harvests grown under controlled environment conditions.

	Temperature °C												
	10/4			16/4			27/10			32/16			
	Harvests			Harvests			Harvests			Harvests			
Cultivar	1	2	Mean	1	2	Mean	1	2	Mean	1	2	Mean	Mean
Fawn	1.46	2.36	1.91	1.55	3.46	2.50	1.70	3.85	2.78	1.67	4.23	2.95	2.54
TFM	1.11	2.16	1.63	1.23	2.94	2.09	1.62	3.75	2.69	1.40	3.25	2.32	2.18
Mean	1.29	2.26	1.77	1.39	3.20	2.30	1.66	3.80	2.73	1.54	3.74	2.64	

[1/] Means of five observations

$LSD_{.05}$ for cultivars = 0.0317
$LSD_{.05}$ for temperature = 0.06
$LSD_{.05}$ for harvest = 0.03
$LSD_{.05}$ for cultivars x temperature = 0.13
$LSD_{.05}$ for cultivars x harvest = 0.06
$LSD_{.05}$ for harvest x temperature = 0.13
$LSD_{.05}$ for cultivars x temperature x harvest = 0.25

Table 8. The effects of temperature on tillering[1/] of two cultivars of tall fescue at two different harvests grown under controlled environment conditions.

	Temperature °C																
	10/4				16/4				27/10				32/16				
	Harvest			%	Harvest			%	Harvest			%	Harvest			%	
Cultivar	1	2	Mean	inc.[2/]	1	2	Mean	inc.	1	2	Mean	inc.	1	2	Mean	inc.	
Fawn	8.4	28.0	18.2	70	17.0	35.6	26.3	52	10.0	31.2	20.6	67	13.0	37.2	25.1	68	22.5
TFM	10.4	19.6	15.0	47	15.0	31.6	23.3	53	10.6	20.8	15.7	49	13.2	22.8	18.0	42	18.0
Mean	9.4	23.8	16.6	59	16.0	33.6	24.8	53	10.3	26.0	18.2	58	113.1	30.0	21.6	55	

[1/] Mean of five observations
[2/] Percent increase in 22 days.

$LSD_{.05}$ for cultivar = .44
$LSD_{.05}$ for temperature = 88
$LSD_{.05}$ for harvest = .44
$LSD_{.05}$ for cultivar x temperature = 1.17
$LSD_{.05}$ for harvest x temperature = 1.17
$LSD_{.05}$ for harvest x cultivar = .88
$LSD_{.05}$ for cultivar x temperature x harvest = 3.52

the second harvest (44 days of growth), Fawn seemed to tiller more rapidly than TFM. The average number of tillers for both harvests across all temperatures was 22.5 and 18 for Fawn and TFM, respectively, which was statistically significant. The percent increase in tillering was higher for Fawn at all temperatures except at 16/4°C, where both cultivars were equal (Table 8).

Both cultivars produced more tillers at 16/4°C followed by 32/16°C. Fawn had a lower percent increase in tillering at 16/4°C than at any other temperature, but still showed over a 50 percent increase in the following 22 days. Templeton et al. (87) reported that lower temperatures were favorable for tall fescue tiller production. The high tillering at 32/16°C might be due to higher light intensity or some internal factor. Although attempts were made to equalize light intensity, the high temperature chamber was still slightly greater than the three other chambers. Also, the time or stage of tiller measurements, and the species tested, might explain the differences in the results. There were harvest x temperature and cultivar x temperature interaction. Work with orchardgrass has shown temperature effects depending on age (69).

Water-Soluble Carbohydrates (WSC)

WSC (consisting of fructosans and free sugars), was significantly greater for Fawn than TFM across harvests and across temperatures (Table 9). The WSC level was significantly greater for the second harvest than the first harvest across temperatures and cultivars. This was expected because the plants were older and may not have needed as much energy for growth (16). Also, plants were more mature in the second harvest so more WSC accumulated. There was a lower percent of WSC in the second harvest material than in the first. Increasing temperatures decreased the WSC levels and this corresponds with work by Smith (80), who found that increasing temperature decreased WSC content in timothy bluegrass.

Fructosan

Fawn was slightly higher in fructosan content across temperatures and harvests. Fructosan content was higher at the two lower temperatures for the first and second harvest for both cultivars. However, TFM in the second harvest at the two higher temperatures was significantly greater in fructosan than in the first harvest, while Fawn was equal in fructosan content. Growth reduction in TFM at higher temperatures might have contributed to the increased

Table 9. Percent water-soluble carbohydrates in dry matter 1/ of two cultivars of tall fescue grown at four temperature regimes for two harvests

	Temperature °C												
	10/4			16/4			27/10			32/16			
	Harvests			Harvests			Harvests			Harvests			
Cultivar	1	2	Mean	1	2	Mean	1	2	Mean	1	2	Mean	Mean
Fawn	34.70	35.10	34.90	25.22	24.88	25.05	7.50	12.92	10.21	8.39	6.60	7.50	19.41
TFM	30.86	29.94	30.40	19.77	19.47	19.62	4.37	10.48	7.42	6.18	5.00	5.59	15.76
Mean	32.79	32.52	32.65	22.49	22.17	22.33	5.93	11.70	8.82	7.29	5.80	6.54	

1/ Mean of five observations.
3/ Harvests occurred at 22 and 44 days

$LSD_{.05}$ for cultivar = .25
$LSD_{.05}$ for temperature = .50
$LSD_{.05}$ for harvest = .25
$LSD_{.05}$ for cultivar x temperature = 1.00
$LSD_{.05}$ for cultivar x harvest = .50
$LSD_{.05}$ for cultivar x temperature x harvest = 2.00

Table 10. Percent fructosans in dry matter 1/ for two harvests of two tall fescue cultivars grown at four different temperature regimes.

	Temperature °C												
	10/4			16/4			27/10			32/16			
	Harvest			Harvest			Harvest			Harvest			
Cultivar	1	2	Mean	1	2	Mean	1	2	Mean	1	2	Mean	Mean
Fawn	19.56	14.83	17.20	15.20	11.35	13.31	3.90	4.01	4.00	1.39	1.28	1.35	8.96
TFM	18.97	13.97	16.83	12.57	10.39	11.48	0.87±	3.71	2.29	0.26	1.97	1.12	7.84
Mean	19.26	14.40	17.01	13.92	10.87	12.39	2.38	3.90	3.14	0.83	1.62	1.23	

1/ Mean of five observations.

$LSD_{.05}$ for cultivar = not significant
$LSD_{.05}$ for temperature = .400
$LSD_{.05}$ for harvest = .200
$LSD_{.05}$ for cultivar x temperature = .800
$LSD_{.05}$ for cultivar x harvest = .400
$LSD_{.05}$ for cultivar x temperature x harvest = 1.601

pool of carbohydrate. There was a significant interaction between temperature and harvest.

Table 10 lists Fawn as being significantly higher in fructosan content than TFM at temperatures of 16/4 and 27/10°C. No differences between cultivars occured at 10/4 and 32/15°C. There were significant differences between temperatures. The lower temperatures had higher fructosan content and the higher temperatures had the lowest fructosan content in both cultivars.

Free Sugar Content

Free sugar content (glucose and fructose) was significantly greater for Fawn than TFM across harvests for each temperature and across temperatures. Free sugar content was higher at the second harvest than the first harvest for both cultivars, except at 32/16°C where it was lower for both cultivars. Table 11 lists free sugar content as being higher at the lower temperatures, at higher temperatures the growing rate was faster and assimilates were apparently being used in the process. The rate of respiration was higher and this could have led to a decrease in free sugar concentration at the higher temperatures. As temperatures increased, free sugar concentration decreased.

Figure 7 shows that as temperature increased, the ratio of free sugar to fructosan increased. Waite (91) reported

Table 11. Percent free sugars in dry matter[1/] for two harvests of two tall fescue cultivars grown at four different temperature regimes.

	Temperature °C												
	10/4			16/4			27/10			32/16			
	Harvests			Harvests			Harvests			Harvests			
Cultivar	1	2	Mean	1	2	Mean	1	2	Mean	1	2	Mean	Mean
Fawn	15.14	20.27	17.70	9.82	13.53	11.68	3.59	9.23	6.41	7.00	5.52	6.25	10.51
TFM	12.44	15.97	14.40	6.95	9.38	8.16	3.57	6.73	5.15	6.16	2.33	4.24	7.94
Mean	13.79	18.12	15.95	8.39	11.46	9.92	3.58	7.98	5.78	6.58	3.92	5.25	

1/ Means of five observations

2/ Twenty-two days between harvests

$LSD_{.05}$ for cultivars = .140

$LSD_{.05}$ for harvest = .140

$LSD_{.05}$ for temperature = .281

$LSD_{.05}$ for cultivar x temperature = .480

$LSD_{.05}$ for cultivar x harvest = .281

$LSD_{.05}$ for harvest x temperature = .480

Table 12. Percent crude protein in dry matter[1/] of two harvests of tall fescue grown at four different temperature regimes.

	Temperature °C												
	10/4			16/4			27/10			32/16			
	Harvests			Harvests			Harvests			Harvests			
Cultivar	1	2	Mean	1	2	Mean	1	2	Mean	1	2	Mean	Mean
Fawn	12.47	15.54	14.00	14.04	14.87	14.46	14.15	19.61	16.88	16.08	17.52	16.80	15.54
TFM	12.82	20.21	16.52	16.07	14.89	15.48	16.02	18.09	17.06	18.14	17.81	17.98	16.76
Mean	12.65	17.88	15.26	15.08	14.88	14.96	15.09	18.85	16.97	17.11	17.67	17.39	

1/ Mean of five observations.

$LSD_{.05}$ for cultivars = .175

$LSD_{.05}$ for temperature = .350

$LSD_{.05}$ for harvest = .175

$LSD_{.05}$ for cultivar x temperature = .697

$LSD_{.05}$ for harvest x temperature = .697

$LSD_{.05}$ for cultivar x harvest x temperature = 1.395

$LSD_{.05}$ for cultivar x harvest = .350.

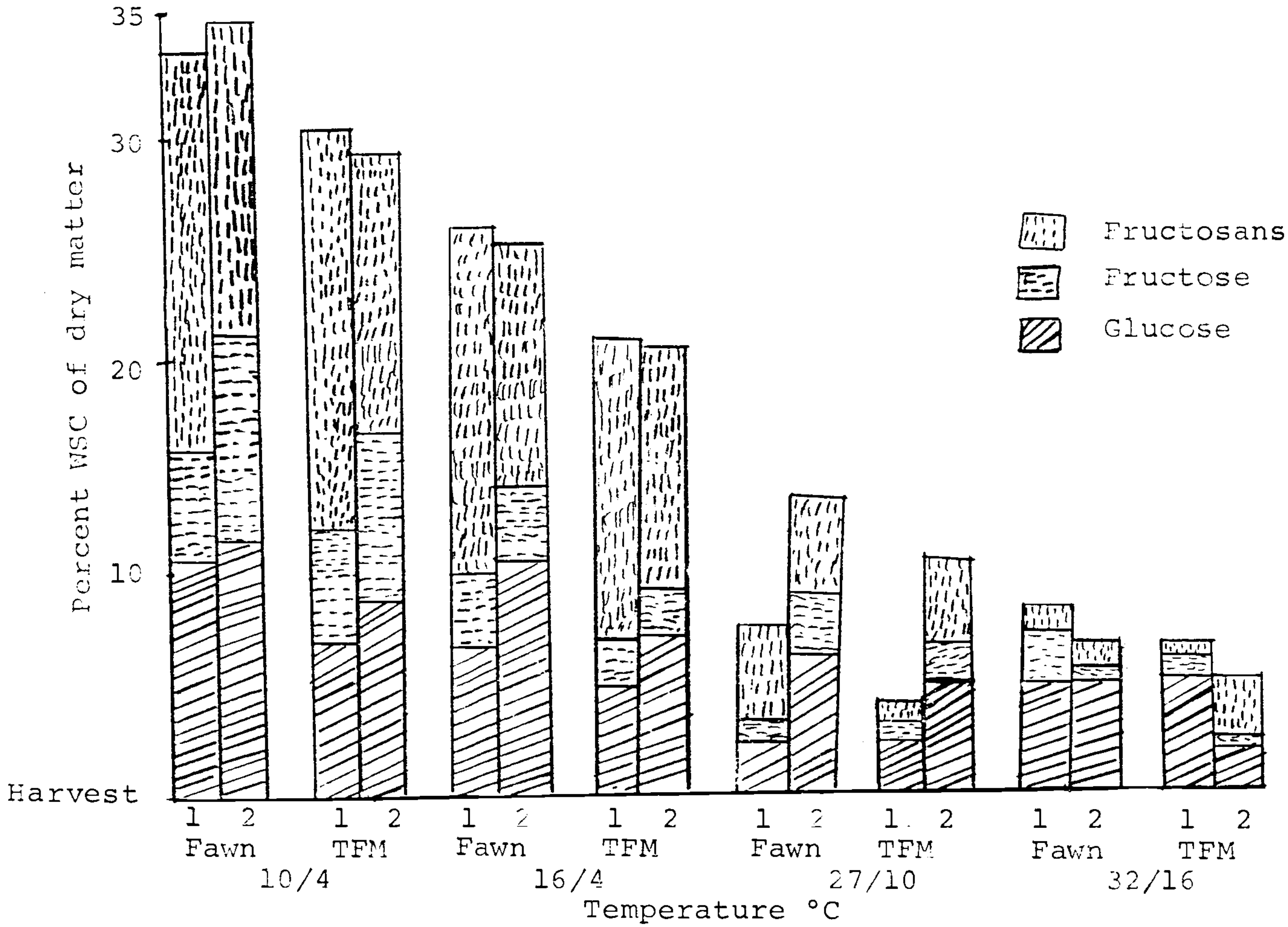

Figure 7. The effect of temperatures on foliage dry matter carbohydrates for two harvests of two cultivars of tall fescue grown in controlled environment.

similar results. He found fructosans to be less of the total WSC content in warm climates than in cold climates.

The glucose fraction was slightly higher than reported (15) and this may be due to retraction techniques, whether this caused inflated free sugar content is subject to question.

Crude Protein Content

Fawn was higher in WSC content than TFM but the opposite was true for crude protein in the dry matter production material for the two harvests. Crude protein increased with increased temperatures. For example, crude protein at temperatures of 10/4 and 32/16°C was 15.26 percent and 17.39 percent, respectively. These results do not follow Beevers and Copper (12) who found that at lower temperatures the percent nitrogen was higher. The amount of protein in the plant tissue not only depends on temperature, but also on growth stage of the plant. It would seem that at higher temperature high metabolism of carbohydrates could favor protein synthesis. In opposition to this theory, the more rapid hydrolysis of protein and faster leaf maturation in warmer temperatures, could decrease the protein content. Table 12 shows the differences between harvests in crude protein across cultivars and temperatures. In all temperatures except 16/4°C, the second harvest is higher in crude protein content than the first. The means of both harvests are very close except at 10/4 and 27/10°C. It would seem unreasonable that the second harvest material would be slightly higher than the first harvest material due to older plants. The increase in crude protein in the second harvest may be due to the synthesized new plant material.

There was no significant relationship between crude protein and carbohydrates in this study. However, a trend is visible. As crude protein increases, WSC decreased, possibly due to protein synthesis. Both cultivars had higher crude protein concentration at 27/10°C and 32/10°C across first and second harvests.

Mean Relative Growth Rate ($\overline{RGR}$)

There were no significant differences in the mean relative growth rates across temperatures. TFM was higher at temperatures 10/4, 16/4 and 27/10°C, while Fawn was significantly greater at 32/16°C (Table 13). These results indicate that Fawn had a faster growth rate than TFM at the highest temperature, while TFM was higher at the lower temperatures. This could be attributed to the differences in growth habits between these two cultivars. No differences between temperatures within cultivars occurred for RGR regrowth from the first and second harvest plants.

Table 13. The effect of temperature on the mean relative growth rate[1/] of two cultivars of tall fescue grown at four different temperature regimes.

	Mean Relative Growth Rate[2/] (mg/dry matter/time)				
	Temperatures °C				
Cultivar	10/4	16/4	27/10	32/16	Mean
Fawn	31.38	36.85	35.88	43.18	36.82
TFM	31.84	39.57	37.31	36.84	36.39
Mean	31.61	38.21	36.60	40.01	

[1/]Mean of ten observations.

[2/]$\overline{RGR} = \frac{\ln W_2 - \ln W_1}{t_2 - t_1}$, the initial and final weight of plant material represented by W_1 and W_2 respectively, over the time intervals t_1-t_2 (22 days).

$LSD_{.05}$ for cultivars = not significant.
$LSD_{.05}$ for temperature = not significant.
$LSD_{.05}$ for cultivar x temperature = 3.77.

Figure 8. The differences in regrowth among four temperature regimes in tall fescue.

Figure 9. The differences in regrowth among four temperature regimes in TFM tall fescue.

Regrowth Dry Matter

TFM did not show differences in growth patterns from Fawn in dry weight matter at the first or second harvest at lower temperatures, but the regrowth results bear out the observed differences between cultivars in the field. These findings suggest that temperature effects these two cultivars' growth rate during the growing season.

TFM produced slightly more regrowth dry matter than Fawn at the two lower temperatures, while Fawn was higher in regrowth dry matter at the two higher temperatures in both regrowth dates (Table 14).

Both cultivars had their highest regrowth dry matter at 27/10, 16/4, 32/16 and 10/4°C, with 2.45 g, 1.32 g, 0.86 g, and 0.55 g/4 observations or pots, respectively. TFM was significantly higher than Fawn at 10/4 and 16/4°C in regrowth dry matter, while Fawn was significantly greater at 27/10 and 32/16°C. Fawn was significantly greater in regrowth dry matter across all temperatures and regrowth dates.

As temperature increased, both 13 and 35 days regrowth dry matter increased except at 27/10 was higher than 32/16°C. Figures 8 and 9 show Fawn and TFM to differ in plant height at various temperature regimes. Fawn and TFM show less growth at 10/4 and 32/16°C, respectively.

Table 14. The effect of temperature on the regrowth dry matter[1/] taken at two dates for two cultivars of tall fescue grown at four different temperature regimes.

	Temperature °C												
	10/4			16/4			27/10			32/16			
	Days Regrowth			Days Regrowth			Days Regrowth			Days Regrowth			
Cultivar	13	35	Mean	13	35	Mean	13	35	Mean	13	35	Mean	Mean
Fawn	0.28	0.71	0.49	0.63	1.84	1.23	2.58	3.38	2.98	1.25	1.13	1.19	1.47
TFM	0.42	0.80	0.61	0.68	2.15	1.41	1.49	2.35	1.92	0.53	0.54	0.53	1.11
Mean	0.35	0.75	0.55	0.65	1.99	1.32	2.03	2.86	2.45	0.89	0.83	0.86	

[1/] Mean of four observations.

$LSD_{.05}$ for cultivar = 0.032
$LSD_{.05}$ for harvest = 0.032
$LSD_{.05}$ for temperature = 0.065
$LSD_{.05}$ for cultivar x temperature = 0.131
$LSD_{.05}$ for cultivar x regrowty = 0.065
$LSD_{.05}$ for cultivar x temperature x regrowth = 0.26

Table 15. Percent fructosan in the regrowth dry matter[1/] of 13 and 35 days of two cultivars of tall fescue grown at four different temperature regimes.

	Temperature °C												
	10/4			16/4			27/10			32/16			
	Days Regrowth			Days Regrowth			Days Regrowth			Days Regrowth			
Cultivar	13	35	Mean	13	35	Mean	13	35	Mean	13	35	Mean	Mean
Fawn	4.38	5.40	4.89	2.41	7.04	4.72	4.10	4.31	4.20	0.53	1.09	0.79	3.65
TFM	1.35	6.13	3.74	1.54	5.56	3.55	3.86	4.84	4.35	0.24	2.60	1.42	3.24
Mean	2.85	5.76	4.31	1.97	6.30	4.13	3.98	4.57	4.28	0.38	1.84	1.10	

[1/] Mean of four observations.

$LSD_{.05}$ for cultivar = not significant
$LSD_{.05}$ for regrowth = 0.144
$LSD_{.05}$ for temperature = 0.287
$LSD_{.05}$ for cultivar x temperature = 0.574
$LSD_{.05}$ for cultivar x regrowth = 0.287
$LSD_{.05}$ for cultivar x temperature x regrowth = 1.148

Water-Soluble Carbohydrates (WSC) in Regrowth

Fructosan and free sugars combined make up WSC content.

Fructosan

There were no differences in fructosan between cultivars across regrowth dates and temperatures.

The 35-day regrowth was higher in fructosan content in all temperatures than at the 13 day regrowth. These results were expected because the 13-day regrowth was new material and was still re-establishing leaf tissue after harvest. At the 35-day regrowth, the fructosan content started to accumulate, presumably because of more leaf area available, which could supply assimilates for storage. Fawn was higher than TFM at the two lower temperatures and TFM was higher than Fawn at the two higher temperatures (Table 15).

The lowest percent fructosan for both cultivars in regrowth dry matter was observed at 32/16°C. This was anticipated due to higher respiration and a lower ratio of photosynthesis to respiration.

Free Sugars in Regrowth

Fawn was significantly greater in free sugars than TFM across all temperatures and regrowth periods. The highest amount of free sugar content for both cultivars was found at 16/4, followed by 10/4, 27/10, and 32/16°C, with concentrations of 18.90, 14.96, 11.29, and 8.77 percent, respectively (Table 16).

The percent free sugar at the 35-day regrowth was significantly higher than for 13-day regrowth for all four temperatures except at 32/16°C.

TFM was higher in free sugar content than Fawn at 16/4°C temperature. There was no cultivar x temperature interaction.

Figure 10 shows the differences in WSC, fructosans, and free sugars in both regrowth dates. The ratio of free sugar to fructosan is higher in regrowth than in the first or second harvest dry matter. Also, the fructosan to free sugar ratio decreased as temperature increased, due to the larger portion of free sugar at higher temperatures. As temperature increased, free sugar made up a larger portion of WSC than fructosan. Table 17 lists the results of 35-day regrowth and shows significantly greater WSC than 13-day regrowth for all temperatures except at 32/16°C.

Fawn had significantly higher WSC at all temperatures in the 13-day regrowth, with the exception of 32/16°C, where TFM was slightly higher. TFM was higher in WSC at temperatures of 16/4 and 32/16°C for the 35-day regrowth, while Fawn was higher at 10/4 and 27/10°C. Perhaps differential utilization for growth could explain this observation.

Table 16. The percent free sugar content in the regrowth dry matter[1/] taken at 13 and 35 days for two cultivars of tall fescue grown at four different temperature regimes.

	Temperature °C												
	10/4			16/4			27/10			32/16			
	Days Regrowth		Day	Days Regrowth			Days Regrowth			Days Regrowth			
Cultivar	13	35	Mean	13	15	Mean	13	35	Mean	13	35	Mean	Mean
Fawn	15.21	17.57	16.39	18.35	21.39	19.87	10.56	14.32	12.44	10.53	7.34	8.94	14.41
TFM	10.37	16.67	13.51	12.40	23.46	17.93	7.61	12.66	10.13	10.63	6.59	8.61	12.55
Mean	10.79	17.12	14.96	15.38	22.43	18.90	9.09	13.49	11.29	10.57	6.97	8.77	

1/ Mean of four observations.

$LSD_{.05}$ for cultivar = 0.192
$LSD_{.05}$ for regrowth = 0.192
$LSD_{.05}$ for temperature = 0.383
$LSD_{.05}$ for cultivar x temperature = 0.766
$LSD_{.05}$ for cultivar x regrowth = 0.383
$LSD_{.05}$ for cultivar x temperature x regrowth = 1.532

Table 17. Percent water-soluble carbohydrates[1/] in the regrowth of 13 and 35 days of two cultivars of tall fescue grown at four different temperature regimes.

	Temperature °C												
	10/4			16/4			27/10			32/16			
	Days Regrowth			Days Regrowth			Days Regrowth			Days Regrowth			
Cultivar	13	35	Mean	13	35	Mean	13	35	Mean	13	35	Mean	Mean
Fawn	19.80	23.05	22.15	20.70	28.38	24.54	13.70	18.23	15.96	11.05	8.50	9.29	17.68
TFM	11.86	22.73	17.20	13.88	29.45	21.66	10.10	17.45	13.78	10.55	9.15	9.85	15.63
Mean	15.24	22.89	19.06	17.29	28.91	23.10	11.90	17.84	14.87	11.00	8.83	9.56	

1/ Mean of four observations

$LSD_{.05}$ for cultivar = 0.30
$LSD_{.05}$ for regrowth = 0.30
$LSD_{.05}$ for temperature = 0.59
$LSD_{.05}$ for cultivar x temperature = 1.180
$LSD_{.05}$ for cultivar x regrowth = 0.59
$LSD_{.05}$ for regrowth x temperature = 1.180
$LSD_{.05}$ for cultivar x temperature x regrowth = 2.360

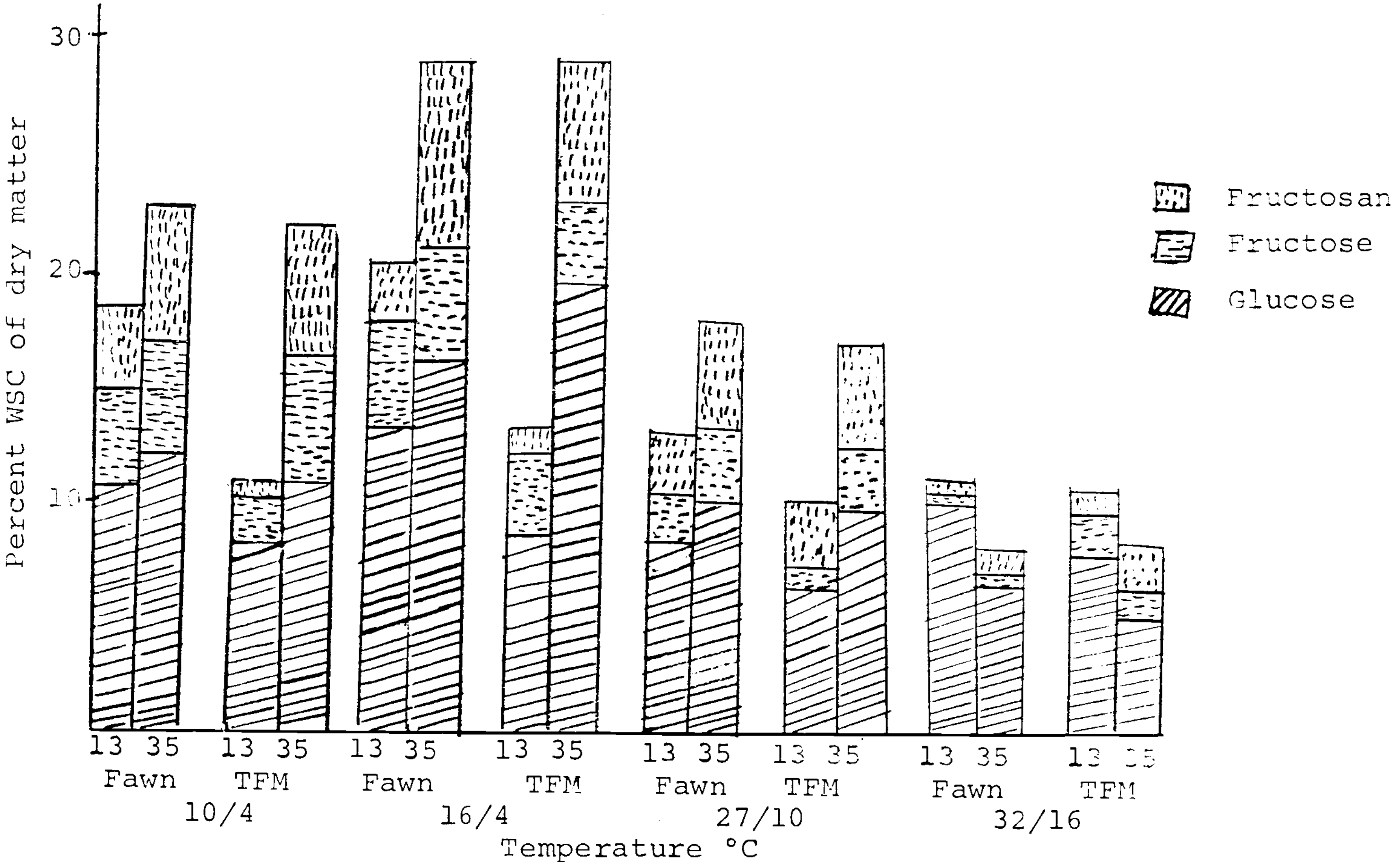

Figure 10. The effect of four temperature regimes on water-soluble carbohydrates on 13 and 35-day regrowth material of two cultivars of tall fescue grown in a controlled environment.

Crude Protein in the Regrowth

TFM was higher in crude protein across temperatures and across regrowth dates. Temperature affected crude protein with the highest percent crude protein at 10/4, followed by 32/16, 16/4 and 27/10°C. The percent protein for the 13-day regrowth was higher than the 35-day regrowth at the two lowest temperatures, and the 35-day regrowth was higher at the two higher temperatures. Both cultivars had the highest crude protein content at 10/4 and 32/16°C (Table 18). At the lower temperatures plant tissue matured more slowly and tended to increase crude protein (12).

Initial Harvest Dry Matter Production versus Regrowth

TFM did not produce more top dry matter at first or second harvest than Fawn as was anticipated, perhaps due to lack of sufficient time for TFM to express its true growth habits. However, at 13-day and 35-day regrowth, TFM produced more regrowth dry matter at lower temperatures than Fawn, while Fawn produced more regrowth dry matter than TFM at higher temperatures.

WSC content in the first and second harvests was higher than in the regrowth at the lower temperatures, but WSC content was higher in regrowth at higher temperatures than first or second harvest material.

Table 18. The percent crude protein in regrowth dry matter[1/] taken in 13 and 35 days of two tall fescue cultivars grown at four different temperature regimes.

	Temperature °C												
	10/4			16/4			27/10			32/16			
	Days Regrowth		D	Days Regrowth			Days Regrowth			Days Regrowth			
Cultivar	13	35	Mean	13	35	Mean	13	35	Mean	13	35	Mean	Mean
Fawn	24.44	26.53	25.49	19.98	17.20	18.59	13.95	14.64	14.29	19.24	21.54	20.39	19.69
TFM	31.76	24.70	28.23	21.84	16.77	19.31	14.09	14.77	14.43	24.09	25.95	25.02	21.75
Mean	28.10	25.62	26.86	20.91	16.99	18.95	14.02	14.70	14.36	21.67	23.75	22.71	

[1/] Mean of four observations.

$LSD_{.05}$ for cultivar = 0.429
$LSD_{.05}$ for regrowth = 0.429
$LSD_{.05}$ for temperature = 0.857
$LSD_{.05}$ for cultivar x temperature = 1.714
$LSD_{.05}$ for cultivar x regrowth = 0.857
$LSD_{.05}$ for cultivar x temperature x regrowth = 3.429

Crude protein was higher for regrowth dates than for first and second harvests across temperatures. This is possible because regrowth material was less mature than first or second harvest.

Roots

Dry Weight

Root dry weight was slightly higher for TFM than Fawn. At 10/4 and 16/4°C TFM showed significantly higher dry root weight than Fawn, but Fawn was significantly greater than TFM at 32/16°C. At temperature 27/10°C, no differences occurred between cultivars (Table 19).

Figure 10 shows the difference in the roots of cultivars grown in vermiculite at greenhouse temperature. Fawn roots were longer than TFM. This might be beneficial for dry summer environments and this might contribute to growth rate differences of these two cultivars during the summer months.

Water-Soluble Carbohydrates (WSC)

WSC in roots was very low in comparison to the first and second harvests and regrowth in WSC content. Fawn was higher in WSC in the roots than TFM at all temperatures (Table 20). The highest concentration for both cultivars was found at the two intermediate temperatures while the two extremes were the lowest.

Table 19. The effect of temperature on the root dry matter (g)[1] of two cultivars of tall fescue grown at four different temperature regimes.

Cultivar	Temperatures °C 10/4	16/4	27/10	32/16	Mean
Fawn	1.36	1.37	1.64	2.20	1.64
TFM	1.61	1.88	1.67	1.90	1.74
Mean	1.48	1.62	1.65	2.05	

[1]Mean of eight observations.

$LSD_{.05}$ for cultivars = not significant.
$LSD_{.05}$ for temperature = 0.080
$LSD_{.05}$ for cultivar x temperature = 0.161

Table 20. The effect of temperature on the percent water-soluble carbohydrates[1] of the roots of two cultivars of tall fescue grown at four different temperature regimes.

Cultivar	Temperatures °C 10/4	16/4	27/10	32/16	Mean
Fawn	3.34	5.37	3.24	2.26	3.41
TFM	0.93	3.87	2.80	2.20	2.45
Mean	2.15	4.62	3.02	2.23	

[1]Mean of eight observations.

$LSD_{.05}$ for cultivars = 0.113
$LSD_{.05}$ for temperature = 0.221
$LSD_{.05}$ for cultivare x temperature = 0.441.

Fructosan

Fawn was also higher in percent fructosans than TFM. The highest fructosan accumulation occurred at the lowest temperatures for Fawn, while TFM was higher at 16/4 and 27/10 and lower at 10/4 and 32/16°C (Table 22).

Free Sugars

Table 23 indicates that Fawn was higher in percent free sugar. The most favorable temperature for both cultivars in free sugar levels was 16/4 and 27/10°C.

Fructosan and free sugar content was much lower in roots than in the foliage. This may be because temperature-origin grasses do not store fructosans in the roots (7).

Root/Shoot Ratio

Table 21. The ratio of top dry matter to root dry weight as affected by temperatures.

	Temperature °C			
	10/4	16/4	27/10	32/16
Roots	1.48	1.62	1.65	2.05
Shoots	1.76	2.30	2.73	2.64
Ratio Shoot/Root	1.19	1.40	1.65	1.29

Root/shoot ratio is affected by temperature. At lower temperatures, the ratio of shoot/root decreases because it favors root growth. The most favorable top growth conditions were 16/4 and 27/10°C. This agrees with Beevers and Cooper (11) who reported that root growth is favored by lower temperatures.

Table 22. Percent fructosan of root dry matter content[1/] for two cultivars of tall fescue grown at four different temperature regimes.

Cultivar	Temperatures °C 10/4	16/4	27/10	32/16	Mean
Fawn	1.74	1.61	0.79	0.36	1.13
TFM	0.25	0.78	0.77	0.34	0.54
Mean	1.00	1.19	0.78	0.35	

[1/]Mean of four observations.

$LSD_{.05}$ for cultivars = 0.039.
$LSD_{.05}$ for temperature = 0.078.
$LSD_{.05}$ for cultivars x temperature = 0.155.

Table 23. Percent free sugar of the root dry matter content[1/] for two cultivars of tall fescue grown at four different temperature regimes.

Cultivar	Temperatures °C 10/4	16/4	27/10	32/16	Mean
Fawn	1.63	3.79	2.45	1.58	2.36
TFM	0.68	3.13	2.04	1.87	1.93
Mean	1.15	3.46	2.25	1.72	

[1/]Mean of four observations.

$LSD_{.05}$ for cultivars = not significant
$LSD_{.05}$ for temperature = 0.197.
$LSD_{.05}$ for cultivars x temperature = 0.394.

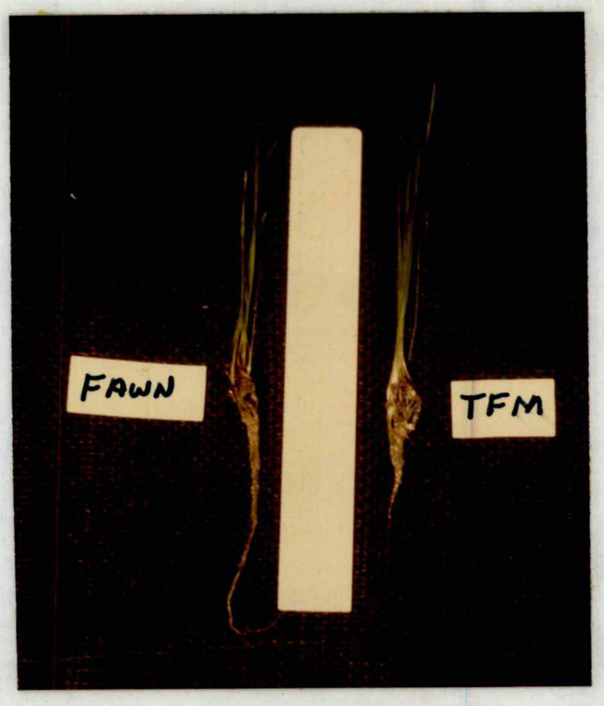

Figure 11. The differences of root length between two cultivars of tall fescue, left (Fawn and right (TFM).

Conclusions

Fawn produced more dry matter in the first and second harvests at all temperatures but when regrowth was observed, TFM produced more regrowth dry matter than Fawn at 10/4 and 16/4°C. Fawn was higher in the regrowth dry matter at 27/10 and 32/16°C. Fawn was higher in WSC, fructosan, and free sugar in dry matter at both regrowth dates. TFM was slightly higher in crude protein. The lowest temperatures resulted in greater accumulation of WSC in both cultivars. The ratio of free sugar to fructosan increased during the regrowth period. Free sugar was somewhat higher than expected (15). Extraction procedures may explain these high concentrations.

Tillering was higher in Fawn than in TFM. Root dry weight was higher for TFM than Fawn, but Fawn had higher amounts of WSC in the roots. Temperature had inconsistent effects on crude protein. The highest level of crude protein occurred at 10/4 and 32/16°C, with the other two temperatures being intermediate. Mean relative growth rate was slightly higher for TFM at the three lower temperatures and Fawn was higher at the highest temperature.

More work needs to be done on the relationship of free sugars and regrowth. The availability of free sugars might explain differences between high and low forage production.

PHYSIOLOGICAL CHARACTERISTICS OF TWO CONTRASTING CULTIVARS OF TALL FESCUE (FESTUCA ARUNDINACEA SCHREB.) GROWN UNDER DIFFERENT TEMPERATURE REGIMES

ABSTRACT

Two cultivars of tall fescue (Festuca arundinacea Schreb.), Fawn and TFM, were grown under day/night temperature regimes of 10/4, 16/4, 27/10 and 32/16°C. Dry matter production, tillering, leaf area, net carbon exchange, dark respiration, and gross photosynthesis, were studied to determine if the above factors were affected by different temperature regimes. These factors were examined for their contribution to the contrasting growth habits of these two cultivars.

TFM was significantly higher than Fawn in dry matter production across temperatures, due to greater dry matter production by TFM at the lower temperatures. At 10/4 and 16/4°C, Fawn produced 5.44 g/pot and 5.90 g, respectively, compared to 10.75 g and 7.37 g for TFM. However, at 32/16°C Fawn produced 8.07 g/pot and TFM produced 6.80 g at 27/10°C, and had the highest dry matter compared to the other three temperatures.

TFM was greater in leaf area per pot at 10/4, 16/4 and 32/16°C, but Fawn was slightly higher at 27/10°C. Leaf area per tiller was similar for both cultivars at 16/4°C,

but TFM was higher at 10/4 and 32/16°C, and Fawn was higher at 27/10°C. There was no cultivar x temperature interaction for leaf area.

Fawn was slightly higher in net carbon exchange in the light at temperatures of 10/4, 16/4 and 32/16°C, while TFM was greater at 27/10°C.

TFM was slightly higher in dark respiration than Fawn at 10/4, 16/4 and 27/10°C. Fawn was significantly higher than TFM at 32/16°C. Dark respiration was lowest at 16/4°C and increased with increasing temperatures.

TFM was higher in gross photosynthesis at 16/4 and 27/10°C, while Fawn was slightly higher at 10/4°C, and significantly greater at 32/16°C. As temperature increased, so did gross photosynthesis in each cultivar.

Dark respiration exceeded net carbon exchange in the light at 32/16°C in both cultivars. Reasons for this are not known, but high temperature, water stress, and increasing senescence may have contributed to the higher dark respiration.

INTRODUCTION

Dry matter usually consists of 90 to 95 percent carbon compounds that are derived directly from photosynthesis.

Loomis and Williams (52) reported that leaf area, its manner of display and CO_2 concentration are two of the major factors contributing to crop yield. Other factors such as leaf shape, size, display of leaves, etc., affect photosynthesis (67). However, environmental factors such as temperature and light intensity (102) affect photosynthesis and ultimately crop yield.

Temperature effects net carbon dioxide assimilation in rice. Murata (65) reported that in rice CO_2 assimilation decreased at temperatures above 40°C. But Azmi and Ormrod (5) found that growing conditions of 40.5/35°C day/night, favored high net CO_2 assimilation for six or eight week old rice seedlings.

Hesketh (43) explained that temperatures of 30°C did not have much effect on growth or leaf assimilation rate in *Triticum aestivum*, *Phaseolus vulgaris*, and *Amaranthus palmeri*, but in *Helianthus annus*, *Zea mays*, and *Gossypium leisutim* photosynthesis was affected at 30°C. Other work by Hew *et al*. (44) showed that the rate of photosynthesis of sunflower decreased when temperature increased from 19 to 34°C. The rate of CO_2 evolution in the light for sunflower and other crops, did not increase with temperature as rapidly as was the case in dark respiration and there was little increase in CO_2 evolution during the light between 30 and 40°C. They found that in all species tested, the rate of photosynthesis decreased markedly at 40°C due to temperature inhibition of photosynthesis and not because of CO_2 evolution.

In bean plants, temperatures of 5°C for a single day inhibited photosynthesis during the following day (30). Treharne et al. reported that orchardgrass grown at 21°C with photosynthesis measured at 29°C had a higher CO_2 assimilation rate than when measured at 21°C (89).

Woledge and Jewiss (102) reported the opposite effect in tall fescue. They observed that leaves grown at low temperatures (10/5) had higher rates of apparent photosynthesis when measured at 10/5 than at 20/15°C day/night respectively. When leaves were grown in the high temperature (20/15°C), the rates measured at 10/5 and 20/15°C were equal. The same workers concluded that the rates of apparent photosynthesis per unit of leaf area in fully expanded leaves differed very little and that temperature did not affect apparent photosynthesis. Rates of apparent photosynthesis per unit dry weight was higher in plants grown at the higher temperature. Leaves grown at the higher temperature, had higher optimum requirement for photosynthesis, but a shorter life span, and a higher respiration rate. Low or high temperatures had little or no effect on the rate of apparent photosynthesis per unit of leaf area, rate of photosynthesis per unit dry weight or respiration in grasses.

Zelitch (105) reported that with increased temperature in C_3 type plants, respiration and photorespiration increases and reduces the overall production of dry matter. Decker (34) reported that photorespiration increased 3.4 fold when the temperature was increased from 17.5°C to 33.5°C. Increased respiration as a result of high temperature is commonly used to explain poor alfalfa growth during July in the Southwest. They hypothesize that high night temperature over a long period of time reduced persistence and yield of alfalfa in Arizona due to increased respiration. The detrimental effect of high night temperature could be excess respiration or a partial destruction of an enzyme of the photosynthesis pathway (35).

An optimum temperature for net carbon exchange for a specific species is similar to the temperature that the plant has been exposed to during the previous few days before measurement (75).

El Sharkawy and Hesketh (38) concluded that temperature optima for net photosynthesis usually occurs at higher temperatures for leaves with higher net photosynthesis. Also rapid net photosynthesis can occur for at least a short time in temperatures of 30 to 45°C. Murata *et al.* (66)

stated that the rate of CO_2 uptake was only slightly affected by temperature between 5 and 30°C, but after 30°C, it increased.

Temperature also affects aging of a plant which in turn affects net carbon exchange. Decker (34) found that net photosynthesis did not increase with increasing temperatures. Young emerging leaves had a lower photosynthetic capacity than fully expanded leaves down the stems (89).

Wilson and Cooper (99) reported that net carbon exchange did not show significant differences in perennial ryegrass genotypes when measured at 15°C after being grown in field conditions, although differences were observed in yield.

There are genetic differences among crop species in leaf photosynthesis. Jewiss and Woledge (49) found that net photosynthesis differences existed among three varieties of tall fescue. Also, Asay _et al_. (3) reported parental progeny differences in net carbon exchange in tall fescue, ranging from 16.4 to 25.8 mg CO_2 $dm^{-2}h^{-1}$.

Hoveland _et al_. (46) believes that net carbon exchange is a poor method of estimating or showing differences in productivity in several cool-season crops because of lack of association between forage yield and net carbon exchange. The lack is due to canopy characteristics and the growth potential of individual tillers.

The purpose of this study was to identify temperature effects on net carbon exchange, dark respiration, tillering dry matter production and leaf area in two cultivars of tall fescue (Festuca arundinacea Schreb.). These studies attempted to explain the basis for the differences in growth between two cultivars, Fawn and TFM.

MATERIALS AND METHODS

Two cultivars of tall fescue (*Festuca arundinacea* Schreb.), Fawn and Oregon TFM were seeded in flats of vermiculite and germinated at 21/10°C. After 30 days, these plants were transplanted into 15 cm pots. These plants were preconditioned in the greenhouse for two weeks at 21/14°C and clipped to 5 cm before being placed in growth chambers at different temperature regimes of 16/4, 27/10 and 32/16°C ± 1°C. A 11.5 photoperiod was used. Light intensity ranged from 1300 to 1800 ft.c. per chamber.

A full strength nutrient solution was applied weekly until a maximum of 144 Kg/ha of nitrogen was added (54).

A completely randomized design with five observations per treatment was used. Net carbon exchange (NCE) in the light and dark respiration (DR) was measured on the plants two months after being placed in the designated temperatures. The whole pot was placed in an air tight flexiglass assimilation chamber in which CO_2 exchange was measured by an infrared gas analyzer (IGA Lira 300). Soil respiration during measurements was excluded by pouring a mixture of four parts parafin and one part mineral oil over the soil. The whole plant was utilized for the measurements of NCE and DR.

Ambient air flowing into the assimilation chamber was at a concentration of 310-340 μg CO_2/liter. The flow rate going into the assimilation chamber was 4-5 liters/min; the air coming out of the chamber into the (IGA) was at 0.8-1.0 liter/min. A 24-point recorder was used to record temperatures, inside and outside the assimilation chamber. Ambient air was conditioned at 25°C in a water bath (83) for a more stable CO_2 concentration.

NCE and DR were monitored and recorded for one minute after peak readings were attained (15 min). Each observation of TFM followed Fawn for each temperature. DR was measured after NCE measurements were completed. A black plastic cover was placed over the assimilation chamber to exclude light. The procedure was repeated and another pot was placed in the chamber until all measurements were completed. NCE and DR were summed and recorded as gross photosynthesis. Plants were harvested after measurements of carbon assimilation, and dry matter, tiller number, tiller weight, and leaf area in cm^2 (sum of leaves, stem and sheath) (see Appendix I), per pot were recorded. Leaf area was determined with a leaf area meter (Lambda L1-3000). Dry weight was obtained by druing in an oven at 70°C to constant weight. Tillers were counted for each pot after the experiment was completed, but initial tiller number was not recorded. Tillers per plant, and weight per tiller were calculated.

NCE and DR were recorded in $mgCO_2dm^{-2}h^{-1}$ (see Appendix I). LSD values were used to test differences among means for cultivars, temperature, and cultivars x temperature interactions.

RESULTS AND DISCUSSION

Dry Matter Production per Pot

Dry matter production was significantly greater for TFM than Fawn when averaged across temperatures. TFM was significantly greater at 10/4 and 16/4°C in dry matter production, while Fawn was significantly higher at 32/16°C. There were no differences between cultivars in dry matter production at 27/10°C (Table 24).

An interaction occurred between temperatures and cultivars due to Fawn growing faster at warmer temperatures and TFM growing better at cooler temperatures (Figure 11). These results were expected because these two cultivars responded differently during the different growing seasons under field conditions (i.e. TFM exhibited faster growth in the fall and Fawn showed a superior growth rate in the summer (Table 2).

There were no differences in dry matter/tiller across temperatures but there were significant differences among temperatures (Table 25). TFM was significantly greater in dry matter/tiller than Fawn at 10/4°C but not at the three higher temperatures.

There were no differences between cultivars in tillering across temperatures (Tables 26 and 27).

Table 24. Dry matter in g/pot of two cultivars of tall fescue grown under four different temperature regimes.

Cultivar	Temperatures °C 10/4	16/4	27/10	32/16	Mean
Fawn	5.44	5.99	8.20	8.09	6.94
TFM	10.75	7.37	8.86	6.81	8.45
Mean	8.10	6.69	8.53	7.45	

$LSD_{.05}$ for cultivars = .24

$LSD_{.05}$ for temperatures = not significant.

$LSD_{.05}$ for cultivars x temperature = .95.

Table 25. The effect of temperature on dry matter per tiller for two cultivars of tall fescue grown at four different temperature regimes.

Cultivar	Temperatures °C 10/4	16/4	27/10	32/16	Mean
Fawn	103.86	97.98	156.20	144.14	125.55
TFM	155.62	107.80	154.92	137.86	139.05
Mean	125.55	102.87	155.56	141.14	

$LSD_{.05}$ for cultivars = not significant

$LSD_{.05}$ for temperature = 10.36.

$LSD_{.05}$ for cultivars x temperature = 41.33.

Table 26. The effect of temperature level on tiller/plant of two cultivars of tall fescue.

Cultivar	Temperatures °C 10/4	16/4	27/10	32/16	Mean
Fawn	11.34	12.06	11.70	12.28	11.85
TFM	13.32	13.60	12.50	11.10	12.65
Mean	12.33	12.83	12.14	11.69	

$LSD_{.05}$ for cultivars = not significant.
$LSD_{.05}$ for temperature = not significant.
$LSD_{.05}$ for cultivars x temperature = 1.80

Table 27. The total number of tillers per pot[1/] for two cultivars of tall fescue affected by temperature.

Cultivar	Temperatures °C 10/4	16/4	27/10	32/16	Mean
Fawn	59.80	61.00	53.20	60.80	58.70
TFM	72.80	74.80	57.40	51.60	64.15
Mean	66.30	67.90	55.30	56.20	

[1/] Mean of five pots.

$LSD_{.05}$ for cultivars = not significant.
$LSD_{.05}$ for temperature = not significant.
$LSD_{.05}$ for cultivars x temperature = 10.85.

Figure 12. The effect of temperature on the growth of TFM and Fawn grown at 10/4°C.

Leaf Area

TFM was higher in leaf area per pot at temperatures 10/4, 16/4 and 32/16°C, with 523.18, 475.95 and 279.14 cm^2 respectively, compared to 328.22, 413.28, and 181.80 cm^2 for Fawn. Higher leaf area for TFM at the lower temperatures was maybe due to wider leaves and thicker stems. Leaf area of Fawn was higher at 27/10°C than TFM (Table 28). The lowest leaf area/pot for both cultivars was found at 32/16°C perhaps due to water stress. No interaction occurred between cultivars and temperature in leaf area/pot, but a significant interaction occurred between cultivars x temperatures for leaf area/tiller.

There were no significant differences in leaf area across temperatures, but significant differences occurred between temperatures.

TFM had higher leaf area/tiller across temperatures. TFM was significantly greater than Fawn at 10/4 and 32/16°C, while Fawn was significantly greater than TFM at 27/10°C. No differences in leaf area/tiller existed between cultivars at 16/4°C (Table 29).

Net Carbon Exchange (NCE)

Fawn was higher than TFM in NCE (CO_2 exchange in the light) across temperatures. As temperature increased, NCE increased. Table 30 lists the findings of 10.06 and 9.89

Table 28. Leaf area (cm^2)/pot[1/] affected by temperature on two cultivars of tall fescue under controlled environmental conditions.

Cultivar	Temperatures °C 10/4	16/4	27/10	32/16	Mean
Fawn	328.22	413.28	445.72	181.80	342.28
TFM	523.18	475.97	411.36	279.14	422.41
Mean	425.70	444.63	428.50	230.52	

[1/] Mean of five observations.

$LSD_{.05}$ for cultivars = not significant.

$LSD_{.05}$ for temperature = 39.03.

$LSD_{.05}$ for cultivars x temperature = 78.06.

Table 29. Leaf area/tiller (cm^2)[1/] of two cultivars of tall fescue affected by four different temperature regimes.

Cultivar	Temperatures °C 10/4	16/4	27/10	32/16	Mean
Fawn	4.34	6.64	8.39	3.23	5.65
TFM	7.40	6.47	7.30	5.79	6.74
Mean	5.87	6.56	7.85	4.51	

[1/] Mean of five observations.

$LSD_{.05}$ for cultivars = not significant.

$LSD_{.05}$ for temperature = .52

$LSD_{.05}$ for cultivars x temperature = 1.04.

for Fawn and TFM $mgCO_2dm^{-2}h^{-1}$ respectively at 10/4°C. Zelitch (105) reported that NCE declined in wheat as temperature increased from 15 to 30°C.

Some of the higher NCE values at the two higher temperatures might have been due to higher light intensity in those two chambers.

Dark Respiration (DR)

There were no significant differences between cultivars across temperatures but significant differences in temperatures and a cultivar x temperature interaction were found. The highest DR concentration for both cultivars occurred at 32/10°C. Fawn was significantly greater than TFM at 32/16°C with a concentration of 26.60 and 14.08 $mgCO_2dm^{-2}h^{-1}$ respectively (Table 31). The lowest DR concentration for both cultivars was found at 16/4°C. TFM was slightly higher in DR at the three lowest temperatures and Fawn was significantly greater at 32/16°C. Dry matter production at the three lowest temperatures was higher for TFM and at 32/16°C dry matter production was higher for Fawn. These findings contradict the assumption that in C_3 plants, as DR increases dry matter production decreases (105). TFM was significantly higher in dry matter production than Fawn across temperatures. This indicates that cultivars with higher respiration produce less dry matter. But both cultivars showed a trend of increasing in dry matter as DR increased (Tables

Table 30. Net carbon exchange[1/] affected by temperature based on leaf area of two cultivars of tall fescue.

Cultivar	Net carbon exchange (mg CO_2 dm^2 h^{-1}) Temperature °C 10/4	16/4	27/10	32/16	Mean
Fawn	10.06	9.30	11.51	14.48	11.34
TFM	9.89	8.89	12.95	10.81	10.64
Mean	10.03	9.09	12.22	12.62	

[1/]Mean of five observations.

[2/]Leaf area consists of leaves, stems, and sheaths.

$LSD_{.05}$ for cultivars = not significant.

$LSD_{.05}$ for temperature = not significant.

$LSD_{.05}$ for cultivars x temperature = not significant.

Table 31. The effect of temperature on dark respiration[1/] of two cultivars of tall fescue grown at different temperatures.

Cultivar	Dark respiration (mg CO_2 dm^{-2} h^{-1}) Temperature °C 10/4	16/4	27/10	32/16	Mean
Fawn	6.56	5.22	7.72	26.60	11.53
TFM	8.34	6.85	8.05	14.08	9.33
Mean	7.45	6.03	7.88	20.94	

[1/]Leaf area consists of leaves, stems, and sheaths.

$LSD_{.05}$ for cultivars = .73.

$LSD_{.05}$ for temperature = 1.45.

$LSD_{.05}$ for cultivars x temperature = 2.91.

25 and 32, respectively). Delaney et al. (35) found an inverse relationship between minimum temperature and minimum DR and this could be explained through the reduction of available substrate resulting from decreased photosynthesis during high temperature periods. Also, it is believed that night temperatures have a greater correspondence to DR than day temperatures.

Leaf area was slightly higher in TFM than Fawn while Fawn was significantly greater in dark respiration across temperatures. Delaney et al. (35) showed that as respiration increased, the yields of alfalfa decreased. This could be attributed to high photorespiration. Decker (34) indicated that photorespiration increased 3.4 fold when leaf temperature was raised from 17.5 to 33.4°C. It was observed at 32/16°C that DR (CO_2 evolution) was higher than NCE (CO_2 uptake in the light). This can suggest that at that moment CO_2 is being used to supply energy for other metabolism such as protein and ATP, necessary for a short while because a plant cannot survive when more CO_2 is given off than taken in. This is an indication of plant senecenses.

Gross Photosynthesis

Gross photosynthesis (sum of NCE and DR) was significantly greater in Fawn than TFM across temperatures. There were significant differences among temperatures. The highest concentration for both cultivars in gross photosynthesis occurred at 32/16°C due to higher DR. There were significant differences at 32/16°C with 41.04 and 24.71 $mgCO_2dm^{-2}h^{-1}$ for Fawn and TFM respectively (Table 32). There were no differences between cultivars at 27/10, 16/4 and 10/4°C temperature regimes. The lowest gross photosynthesis concentration for both cultivars occurred at 16/4°C. There was a cultivar x temperature interaction due to TFM being slightly higher than Fawn in gross photosynthesis at 16/4 and 27/10°C and TFM was lower than Fawn in gross photosynthesis at 10/4 and 32/16°C.

Gross photosynthesis was higher at the two higher temperatures for both cultivars. Fawn was twice as high as TFM in gross photosynthesis and dark respiration at 32/16°C. At this temperature, Fawn was higher in dry matter production than TFM.

Conclusions

Temperature affected the dry matter production of the two cultivars. TFM was significantly greater than Fawn due to faster growth at the three lowest temperatures.

TFM was slightly higher than Fawn in leaf area/pot and leaf area/tiller across temperatures because of wider width and thicker stems.

There were no differences in NCE between cultivars and among temperatures. Dark respiration and gross photosynthesis were significantly greater for Fawn than TFM across

Table 32. The effect of temperature on the gross photosynthesis[1/] of two cultivars[2/] grown at four different temperature regimes.

Cultivar	Gross photosynthesis ($mg\ CO_2\ dm^{-2}\ h^{-1}$) Temperatures °C 10/4	16/4	27/10	32/16	Mean
Fawn	19.04	14.61	19.22	41.04	23.48
TFM	18.23	15.75	20.99	24.71	19.92
Mean	18.64	15.19	20.04	32.88	

[1/]Leaf area consists of leaves, stems, and sheaths.

[2/]Mean of five observations.

$LSD_{.05}$ for cultivars = .78.

$LSD_{.05}$ for temperature = 1.96.

$LSD_{.05}$ for cultivars x temperature = 3.92.

temperatures. There were significant differences in gross photosynthesis and dark respiration between cultivars at 32/16°C. But no differences existed between cultivars at the three lowest temperatures in DR or gross photosynthesis.

It was found that NCE was lower than DR at 32/16°C in both cultivars. Higher temperature and less moisture in the leaves may have caused the plants to respire faster. Also, at that temperature more leaf senescences may have occurred.

Fawn respired at a faster rate in higher temperature than TFM and TFM tended to respire faster than Fawn at three lower temperatures. In these findings it suggests that dark respiration rate may be associated with high yield if enough carbon metabolate are supplied for protein, lipid, nucleic acids, synthesis, etc., Also, the higher gross photosynthesis for Fawn was higher in dry matter production, but TFM at the two lower levels of gross photosynthesis had the two higher dry matter production.

INFLUENCE OF TEMPERATURE REGIMES ON PERLOLINE AND CRUDE PROTEIN CONTENT OF TWO CULTIVARS OF TALL FESCUE

ABSTRACT

Tall fescue (Festuca arundinecea Schreb.), Fawn and TFM, which differ in growth habit, were grown at different temperatures to determine if temperature levels would influence the perloline and crude protein concentration in these two cultivars.

Perloline (an anti-quality component) which has been implicated in poor animal influence on tall fescue, especially during the summer months and protein (a quality component) levels in forage, may be affected by temperature thus altering the quality of forage.

Fawn, a commercial cultivar since 1964, is a good forage producer in the Willamette Valley but does not grow as well as TFM, an experimental line, during the fall months.

Fawn, an eight-clone synthetic and TFM, a twelve-clone synthetic, developed by the Oregon Agricultural Station, Corvallis, Oregon (39), were grown at day/night temperatures of 10/4, 16/4, 27/10 and 32/16°C, and total nitrogen and perloline concentrations were determined.

The highest concentration of perloline in both cultivars was found at 27/10 followed by 32/16°C temperature.

Fawn was significantly higher in perloline than TFM at every temperature level. It was interesting to note that perloline content was higher in Fawn at 27/10°C, which was the most favorable temperature for growth of Fawn. TFM showed the highest perloline concentration at 32/16°C, while growth was favored at lower temperatures.

Fawn and TFM showed the highest concentrations of crude protein at 27/10 and 10/4°C temperatures, respectively. TFM was slightly higher in crude protein than Fawn for all the temperatures except at 27/10°C. Crude protein concentration was higher at the higher temperatures. There was no significant relationship between crude protein and perloline concentration.

INTRODUCTION

One important problem involving tall fescue (Festuca arundinacea Schreb.) is poor performance of livestock grazing tall fescue especially during the summer months (24, 26, 40). This poor performance in animals grazing tall fescue has been attributed to inhibition of cellulose digestibility and volatile fatty acid production by alkaloids (27). Perloline, an alkaloid formed in Festuca and Lolium species is believed to be derived from tryptamine (31).

Bush and Buckner (26) observed that gains in cattle during July and August were inversely related to the concentration of perloline in tall fescue. The inhibiting effect of perloline on nutrient digestibility under pasture grazing conditions may decrease forage intake and further contribute to reduced performance (17, 26). Inhibiting the microflora activity and cellulolytic activity in the rumen decreases the energy availability to the animal (17, 24, 25, 27).

There are many factors which may affect not only antiquality components such as alkaloids, but also quality factors such as protein concentration in tall fescue. Gentry et al. (40) found that alkaloid concentration in tall fescue herbage managed as pasture was related to season, varieties and the amount of nitrogen applied. Marten et al.

(58) reported that shading of plants increased the alkaloid concentration, but day length did not influence alkaloid concentration. During the season the alkaloid concentration increased somewhat from early spring to mid-July. A sharp rise occurred during a 17 day period in early August. Perloline concentration during these summer months have been observed at levels of 3000 μg/g of dry weight, 6,700 μg/g in dry weight in commercial varieties and 11,900 μg/g dry matter in breeding material (26).

Moore et al. (64) and Oram (70) found that environment had an influence on the alkaloid concentration depending on the species tested. High temperature on some grasses (*Phalaris* spp.) increased the alkaloid concentration, while in others it didn't have much effect. Usually a genotype by temperature interaction occurred in most species tested. These same workers found that low light, temperature above 20°C and moisture increased the concentration of alkaloids in *Phalaris aquatica* (64, 70). Also, Marten et al. (58) found that two strains of *Phalaris aquatica* had much higher levels of alkaloids in autumn than in winter; the autumn environment had higher temperatures, higher light intensities, longer days, and more severe moisture stress. An increase in nitrogen fertilization increased the concentration of perloline. However, ammonia-nitrate had a more adverse effect than urea (25).

Gentry *et al*. (41) found cultivars in tall fescue to differ in perloline concentrations. Kenwell cultivar had the highest concentration of perloline followed by Ky 31 and Alta. They showed significant differences among varieties, fertilization, and sampling dates.

Perloline concentration varies within parts and age of plants. Leaves contain twice as much perloline concentration as other parts of the plant. Gentry *et al*. (41) reported a 44 percent decline in matured leaves compared to young leaves and 61 percent more in leaves than in stems. Older plants are 20 times higher in perloline if no nitrate was applied (8). The number of alkaloids was greater in mature plants but less quantity of each kind was noted. Also, only traces were observed in high alkaloid material when the material had been hay-cured (41).

Perloline was the principal alkaloid in seedlings of all varieties of tall fescue tested (24).

Crude protein content, a quality component (21), depends chiefly on the time of cutting or growth stage at harvest, level of N fertilization of grasses, and leaf content. Factors such as temperature and nitrogen effect crude protein as well as perloline content (9, 41). Nitrogen application increases the protein and perloline content of forage grasses (10). Buckner *et al*. (23) concluded that protein was the lowest during the hot dry summer months, when the grass had not received nitrogen fertilization.

Protein was highest during cool damp conditions in early spring after nitrogen fertilization. Protein content in tall fescue ranged from 13.7 to 29.7 percent.

The primary objective of the study was to determine if temperature levels would affect perloline concentration in the two distinctively different cultivars of tall fescue. Crude protein was also examined as an important quality component and the relationship between perloline and crude protein was evaluated.

MATERIALS AND METHODS

Two cultivars of tall fescue (Festuca arundenacea Schreb.), Fawn and Oregon TFM, were seeded in flats of vermiculite and germinated at 21/10°C. After 30 days these plants were transplanted in 10 cm pots.

These plants were preconditioned in the greenhouse for two weeks and clipped to five cm before being placed in growth chambers at different temperature regimes of 10/4, 16/4, 27/10, and 32/16°C. Photoperiod was 11.5 with 12.5 hours of light/dark respectively. Each chamber ranged from 1300 to 1800 ft.c. in light intensity. A completely randomized design with four observations per treatment was used.

A full strength nutrient solution was used until a maximum of 144 kg/ha of nitrogen was applied (54).

After 44 days, the dry matter production of each cultivar was harvested and dried at 70°C for 48 hours before being ground to pass a 40-mesh screen. These samples were kept 15-20 days in metal containers and re-dried before perloline and total N were determined.

Peroline analysis was determined by the method of Shaffer et al. (78) and total N, by the method of Nelson and Sommers (68). Total N was reported as protein (% N x 6.25). Perloline and crude protein levels were analyzed statistically.

RESULTS AND DISCUSSION

Perloline

Fawn was significantly greater in perloline concentration than TFM at every temperature (Table 34).

Fawn showed the highest concentration at 27/10°C, which also was the most favorable for dry matter production (Table 8), followed by 32/16, 16/4 and 10/4°C. TFM was very low in comparison to Fawn, and showed the highest concentration at 32/16 followed by 16/4, 27/10 and 10/4°C. The highest concentration for Fawn and TFM was 1103 μg/g and 45.59 μg of dry material, respectively (Table 33).

Perloline content is believed to be hereditable and there are differences among tall fescue varieties (31). Even though Fawn is high compared to TFM, it is still low in comparison to other varieties of tall fescue (16). Perloline in pasture of tall fescue has been known to reach to 3000 μg/g per dry material on mature stands (41) and young animals have to ingest 25 to 50 g/day of perloline to be harmful (24).

High temperature tended to increase perloline concentration in the plant material. Temperatures were observed to cause more noticeable differences in Fawn than in TFM. This may be due to the fact that there is less alkaloid in TFM to be affected.

Perloline levels at higher temperatures were significantly greater than at lower temperatures (Table 33).

Fawn was higher in perloline at 27/10 than 32/16°C. It is conceivable that above a certain temperature, perloline concentration decreases in certain cultivars but not in others due to growth rate differences or differences in leaf-to-stem ratios.

Cultivars such as Fawn, at higher temperatures may be shunting nitrogen compounds to protein synthesis, instead of using them for perloline synthesis. At 27/10°C chamber, light intensity was slightly lower than at 32/16°C, and this might have affected the perloline concentration. TFM produced more dry matter (Table 8) at 27/10°C, but perloline content was lower than either temperatures of 32/16 or 16/4°C. TFM varied in perloline concentration from 3.30 μg/g to 45.6 μg/g, while Fawn varied from 118.9 μg/g to 1103.1 μg/g in seedling dry material.

Gentry (41) showed that during the summer months the perloline level increased to its highest concentration. This might be due to temperature level because light and growth rates during the summer were assumed to be highest, and perloline is believed to increase at lower light intensities.

Crude Protein

There were no differences between Fawn and TFM in crude protein content across temperatures. TFM was greater at 10/4°C than at other temperatures. This supports the work of Beevers and Cooper (12) who found total N to be higher at lower temperatures. The highest amount in crude protein content for Fawn was at 27/10 followed by 32/16°C because of the faster growth rate of Fawn at these two temperatures. TFM was lower in crude protein at temperatures of 16/4°C, with a concentration of 14.42 percent (Table 34).

When nitrogen is not limiting, both nitrogen and perloline content tend to increase. The highest crude protein across cultivars occurred at 27/10°C, which was significantly greater than the three other temperatures. The lowest concentration of crude protein was at 16/4°C for both cultivars.

Perloline and Crude Protein Interrelationships

TFM was slightly higher in crude protein, but Fawn was significantly greater in perloline at the four temperatures tested. Crude protein and perloline both increased in Fawn as temperature increased, except at 32/16°C, where these chemical components were lower than at 27/10°C. TFM had the highest concentration of crude protein at the lowest

Table 33. The effect of temperature on perloline concentration in ug/g of dry material[1] of two cultivars of tall fescue under different temperature regimes.

Cultivar	Temperatures °C 10/4	16/4	27/10	32/16	Mean
Fawn	118.88	198.75	1103.13	317.36	434.53
TFM	3.30	12.58	8.06	45.59	17.38
Mean	61.09d	105.67c	555.59a	181.48b	

$LSD_{.05}$ for cultivars = 9.49.

$LSD_{.05}$ for temperature x cultivar = 37.99.

Table 34. The effect of temperature on the percent crude protein[1] of two cultivars of tall fescue grown at four different temperature regimes.

Cultivar	Temperatures °C 10/4	16/4	27/10	32/16	Mean
Fawn	14.97	14.28	19.57	17.43	16.56
TFM	20.59	14.42	18.37	18.46	17.99
Mean	17.83b	14.35c	18.97a	17.95b	

[1]Mean of four observations.

$LSD_{.05}$ for cultivars = not significant.

$LSD_{.05}$ for cultivars x temperature = not significant.

Means within columns that have the same letters don't differ at .05 level of p according to Keul's multiple range.

temperature and perloline was at the highest concentration at the highest temperature. Fawn was higher in both crude protein and perloline due to a faster growth rate at higher temperatures. A faster rate of growth also increased perloline content (20, 41).

Temperature effects were not as predictable above 20°C in perloline as protein since there is a significant genotype x temperature interaction for perloline (64, 70), A significant interaction between cultivar x temperature for perloline, but not for crude protein occurred in this study.

It was noticed in the field that (95) when nitrogen fertilization was at a minimum, protein decreased and perloline increased slightly. This may be because perloline has a greater sink for nitrogen compounds available when competing for these nitrogen compounds. If nitrogen was not limiting, then both perloline and crude protein may increase.

Conclusions

Temperature influences the concentration of perloline. The higher temperature had the higher concentration of perloline. There was an interaction between cultivars x temperature. Not all cultivars are affected the same by temperature. Fawn was significantly higher in perloline across temperatures. TFM was higher in crude protein content than

Fawn across temperatures. TFM accumulates more crude protein in cooler temperatures, while Fawn was higher in crude protein at warmer temperatures.

SUMMARY AND CONCLUSIONS

Field and growth chamber experiments were performed to describe and determine the basis for the differential growth characteristic during the season for Fawn and TFM, tall fescue. The effect of four different temperature regimes on photosynthesis, dark respiration, tillering, dry matter, carbohydrates, crude protein, and perloline an anti-quality component, were also measured.

Field Studies

Fawn produced more dry matter over three harvests than TFM. Fawn was higher in WSC across the seven month period. TFM was higher in crude protein than Fawn under field conditions. Stems were higher in WSC content but lower in crude protein than leaves. At lower growth rates, both cultivars accumulated more WSC but less amounts of crude protein content.

There was a negative relationship between WSC and crude protein in stems and leaves across the seven month period. WSC decreased and crude protein increased after harvest or nitrogen fertilization. These results suggest that apparently competition for carbon compounds between synthesis of WSC and crude protein occurred. It is believed that WSC's supply carbon skeletons for amino acids to form protein.

Fawn was higher than TFM in tillering but not significantly so under field conditions. Tiller sizes and height were greater for TFM than Fawn in April but in September, Fawn was higher in both tiller size and plant height.

Fawn seemed to have had a faster growth rate during the spring and summer months than TFM.

Growth Chamber Studies

Fawn was significantly higher than TFM in dry matter across harvests and across the four temperature regimes. In the regrowth dry matter, TFM was higher at the two lower temperatures and Fawn was higher at the two higher temperatures.

Fawn was higher in WSC, fructosans, and free sugars than TFM. Levels of WSC were higher at the lowest temperature across first and second harvests and across regrowth dry matter.

Percent WSC and fructosans were higher at the first and second harvests when compared to regrowth at the lower temperatures, but there were small differences between harvests and regrowth in fructosans at the higher temperatures. At the higher temperatures, the percent WSC was higher in regrowth than at first or second harvests.

The concentration of free sugars was higher in regrowth dry matter material than first or second harvest at the two higher temperatures.

Crude protein content increased with increased temperature across cultivars in the first and second harvests, but in the regrowth, crude protein was higher at both 10/4 and 32/16°C followed by 27/10 and 16/4 for both cultivars.

Root dry weight was higher for TFM than Fawn. The WSC content of roots was also higher in Fawn than TFM across temperatures.

TFM was slightly higher in mean relative growth rate at the three lower temperatures and Fawn was significantly higher at the highest temperature.

No differences existed in net carbon exchange in the light between cultivars. Fawn was significantly greater in dark respiration than TFM at 32/16°C but no differences occurred at the three lower temperatures between cultivars. There were differences in gross photosynthesis (summation of net carbon exchange and dark respiration) among temperatures and treatments, but not between cultivars. There was a cultivar x temperature interaction.

TFM was higher in leaf area at 10/4, 16/4 and 32/16°C temperatures, and Fawn was greater at 27/10°C temperature.

Fawn was significantly greater in tillering across harvests and temperatures. The most favorable temperature across cultivars and harvests was at 16/4°C.

Perloline, an alkaloid found in tall fescue, was affected by temperature. There was a cultivar x temperature interaction. Fawn was significantly greater at every temperature and across temperatures in perloline content. The highest concentration of perloline for Fawn was at 27/10°C and for TFM at 32/16°C.

It is possible to conclude that Fawn is higher in forage production during spring and summer months than TFM maybe due to higher temperatures because it stores more WSC, is slightly higher in NCE, dark respiration, and gross photosynthesis. Also, Fawn was higher in tillering than TFM. Fawn was slightly higher in leaf area than TFM at 27/10°C and this could explain the increase in gross photosynthesis at that temperature.

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APPENDICES

APPENDIX I

EXPLANATIONS AND FORMULAS USED IN PHOTOSYNTHESIS STUDY

NCE = photosynthesis - (dark respiration + photosynthesis)

To measure NCE is very simple. The plant is put in an air-tight assimilation chamber and CO_2 concentration is measured entering the chamber in the light, and knowing the air flow rate, a person can determine NCE by:

$$NCE = \text{air flow rate (l/min.)} \times [CO_2 \text{ out} - CO_2 \text{ in } (mgCO_2/l)]$$

Infrared gas analyzer (IGA) is used to determine the CO_2 concentration of the air stream and is expressed in $ulCO_2$ or ppm. This concentration in ul/lCO_2 can be converted to mg CO_2/liter by:

$$mg\ CO_2/l = \frac{ul\ CO_2}{liter} \times \frac{273\ K}{temp.} \times \frac{\text{barometric press.}}{1013\ mb} \times \frac{44{,}000mg}{mole\ CO_2} \times \frac{mole\ CO2}{22.41\ CO_2} \times 10^{-6}$$

One method to standardize the NCE rate is to divide by the leaf area into the mg CO_2 of NCE. This gives you mg $CO_2 dm^{-2} h^{-1}$.

Dark Respiration

Dark respiration provides energy for the essential biochemical reactions concerned with growth and the synthesis of ATP (105).

Dark respiration measures the net carbon exchange in the dark. It is measured in the same manner as was previously described for NCE, which is net carbon exchange in the light.

Gross Photosynthesis

Gross photosynthesis is the summation of both NCE and DR. The calculations for dark respiration were arrived at with the formulas as for NCE and dark respiration.

True photosynthesis is a very difficult parameter to measure so gross photosynthesis was used instead, because photorespiration was measured.

APPENDIX II

EXTRACTION AND ESTIMATION OF SOLUBLE CARBOHYDRATES FROM TALL FESCUE EXTRACTED BY ANTHRONE

Article: Yemm, E. W., and A. J. Willis. The estimation of carbohydrates in plant extracts by anthrone. Biochem. J. 57:508-514. 1954. Dreywood, R. 1946. Industr. Eng. Chem. Anal. 18:499.

A. Extraction - For Percent of Total Nonstructural Carbohydrates

1. Dry and grind samples to pass a 40-mesh screen.
2. Weigh out a sample and place it in a 50 ml Erlenmeyer flask. Between 50-100 mg proves to be the best sample size.
3. Add 30-50 ml of distilled H_2O to each flask.
4. Place flasks on a shaker for 1-2 hours. Use 25°C to keep flasks at room temperature.
5. Filter samples through Whatman #1 filter paper into 50 ml Folin-Wu tubes.
6. Rinse flasks with distilled H_2O and add it to the Folin-Wu tubes.
7. Bring volume up to 50 ml with distilled H_2O.

B. To Extract Free Sugars - such as glucose-fructose and sucrose

1. Use dried and ground samples (the same material as for extraction of TNC).
2. Weigh 50-100 mg, put in 50 ml Erlenmeyer flask.
3. Add 20-30 ml of 85 percent or 90 percent ethanol.

4. Shake for one hour.

5. Filter samples through Whatman #1 filter paper into some Folin-Wu tubes. Rinse flasks with 85 percent to 90 percent ethanol and add it to the Folin-Wu tubes.

   Note: Use the same anthrone reagent and reaction conditions as for extraction of percent TNC.

   Note: If you are interested in looking only for fructosans, use the same material from the ethanol extraction, after filtered, add 30-50 ml percent distilled H_2O to each flask, and follow the same reaction procedure as for percent TNC.

   Note: The O.D. 620 reading that you get plus find the regression number to convert it to ug of both glucose and fructose. Need to have two standard curves - (1) fructose, and (2) glucose.

6. Use two sets of 10 ml of reagents with the same amount of (aliquot) solution and H_2O. To one set boil it for three minutes (fructose to the other set, boil it ten minutes). Add them together to get percent of free sugars.

   Note: Free sugars + fructosan + some starch = percent TNC.

Anthrone reagent

Take 100 ml of 70 percent H_2SO_4, add 0.2 grams of anthrone; or with 50 Oml of 70 percent H_2SO_4 , add 1.0 grams of anthrone.

Note: Make fresh anthrone mixture over 12 hours or place a large quantity of anthrone mixture in the freezer for a couple of weeks.

Reaction conditions (estimation)

1. Add 10 ml of anthrone reagent to each tube.
2. Put the tubes in iced H_2O and cork them.
3. Add 0.1-0.3 ml aliquot of the sample to the top of each test tube, then add distilled H_2O to make up 1.0 ml; i.e., if use 0.1 ml of a sample, add 0.9 ml of distilled H_2O to bring up to 1.0 ml.

   Note: Keep the tubes in iced H_2O.
4. Shake tubes before boiling.

   Note: Samples start to turn yellow to green during boiling.
5. Heat the tubes for exactly three minutes for fructosan, ten minutes for glucose after the H_2O reacted boiling.
6. Take the tubes from the boiling H_2O and ice them immediately. Put the tubes in tap H_2O for a couple of minutes to bring up to room temperature.
7. Shake well before reading. If left for more than five minutes, shake again.

8. Read. Spectrophotometer at wavelength 620 and slit width at 0.5 mm.

Note: Slit width at 0.5 mm not necessary.

Use a Standard

Use a standard tube with each (run) batch of tubes. This standard solution is a known quantity of fructose sugar. Check on your standard curve.

Blank Prepared as Follows:

10 ml of 70 percent anthrone reagent and 1.0 ml of distilled H_2O.

Note: Blank should be yellow after boiling.

Calculations for Percent TNC

Based on Tony Fino Standard Curve

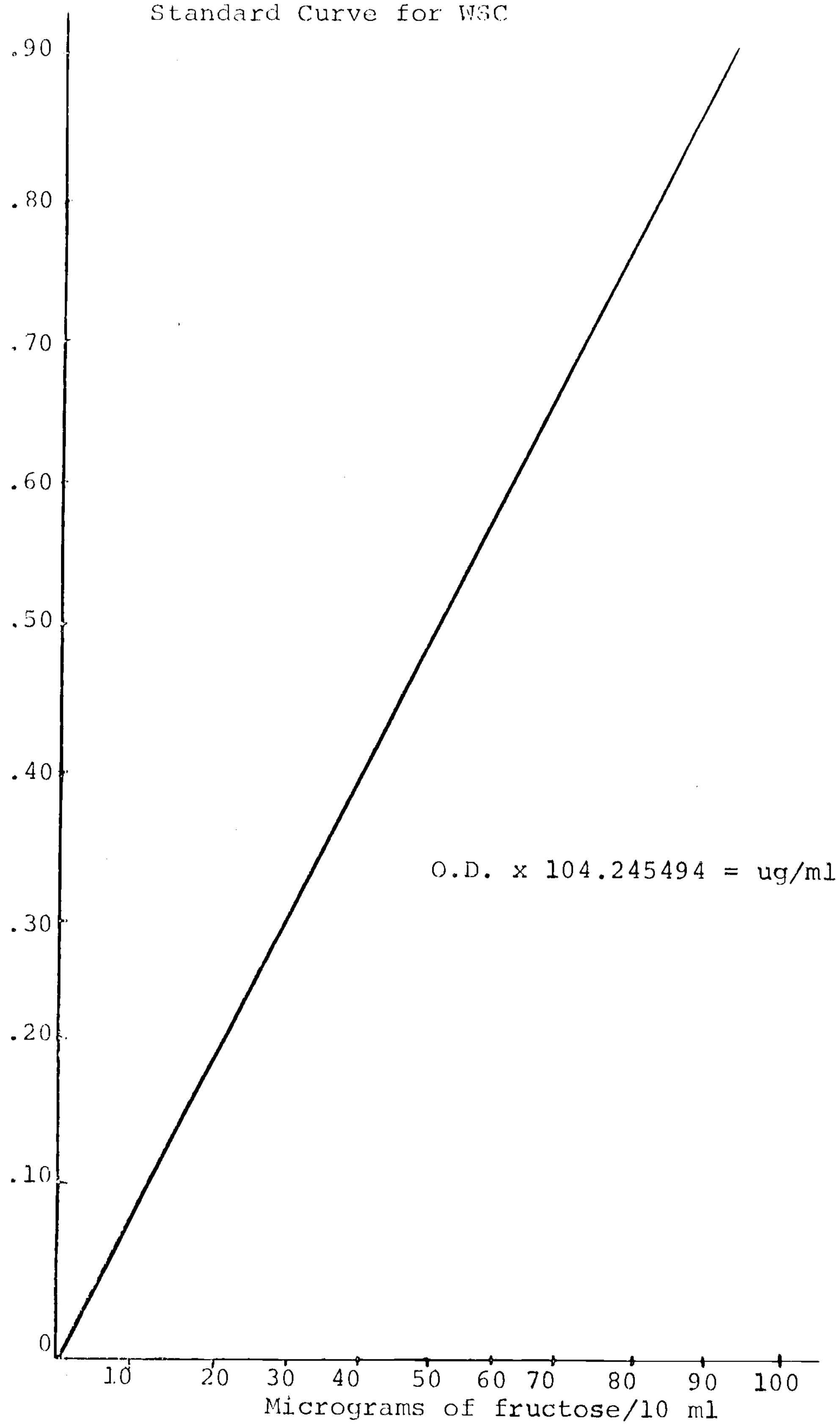
OD_{620} x 104.245945 = ug in sample

$$\frac{\text{ug in sample} \times 0.001 \times \text{DF}}{\text{dry wt (mg)}} = \text{percent TNC}$$

Note: DF = Dilution Factor

To find DF: Example, if use 0.2 ml of sample and bring it up to 1 ml with distilled H_2O, dilution is five times - samples already have been diluted 50 times - total is 250 DF.

My dilution was 500 DF (0.1 ml of aliquot solution).


Standard Curve for WSC
.90
.80
.70
.60
.50
.40
.30
.20
.10
0
10
20
30
40
50
60
70
80
90
100
Micrograms of fructose/10 ml
O.D. x 104.245494 = ug/ml

Appendix 3. Mean squares and levels of significance for dry weight, water-soluble carbohydrates, and crude protein on three harvests material, and the variation of water-soluble carbohydrates and crude protein over a seven month period, Corvallis, Oregon, 1975.

	Three Harvest Analysis		Mean Squares and Levels of Significance							
					Percent WSC			Percent Crude Protein (C. P.)		
Source of Variation	d. f.	Dry Weight	% WSC	% C. P.	d. f.	Stems	Leaves	d. f.	Stems	Leaves
Cultivar	1	3.64(g)**	2.099ns	1.723ns	1	14.338ns	0.496ns	1	0.382ns	1.463ns
Replications	3	0.20ns	9.059ns	2.681ns	3	12.646ns	10.632ns	3	3.000ns	12.612ns
Error (a)	3	0.023	9.596	1.600	3	12.130	7.558	3	0.540	4.007
Harvest	2	35.145**	39.837*	7.657*	11	220.021**	159.683**	5	45.814**	150.562**
Cult. x Har.	2	0.565ns	16.991ns	1.419ns	11	11.821ns	11.975*	5	1.156ns	6.545ns
Error (b)	12	0.269	6.913	1.742	66	9.216	4.844	30	1.639	4.201
(a) C.V.		3.7%	36.9%	17.9%		18.3%	26.6%		14.4%	17.4%
(b) C.V.		12.8%	31.3%	17.2%		15.9%	33.3%		25.0%	16.9%
Cultivar		0.01	1.26	0.10		0.07	0.06		0.03	0.08
Cultivar x harvest		0.13	0.66	0.26		0.75	0.55		0.32	0.51

n.s., *, **, not significant, at .05 or .01 level, respectively.

Appendix 4. Mean squares and levels of significance for dry weight, tillers, carbohydrates, and protein for Fawn and TFM grown at four different temperature regimes for two cultivars and two harvests.

		Mean Squares and Levels of Significance					
Source of Variance	d.f.	Dry wt.	Tillers	% WSC	Fructose	Free Sugars	% Crude Protein
Cultivars	1	2.4851**	414.050**	267.143**	25.1328ns	132.3037**	29.8168*
Temperatures	3	3.7794**	267.483*	2989.151**	1107.8522**	489.5902**	29.2946**
Harvests	1	63.5105**	5216.450**	17.177ns	39.1720**	104.4702**	109.7461**
Cultivar x temperature	3	.2570ns	18.083ns	12.7659ns	3.0400ns	6.2772ns	4.6763ns
Cultivar x harvest	1	.1901ns	451.250**	0.300ns	11.0707ns	18.5474*	2.5418ns
Temperature x harvest	3	16.5892**	9.883ns	53.666**	46.7638*	56.1699**	33.1882**
Cult. x har. x temp.	3	.1755ns	35.55ns	1.085ns	1.9254ns	0.4160ns	14.7202ns
Error	64	.2012	38.738	12.508	8.0166	3.9354	6.1152
CV		15.3%	30.7%	20.1%	33.7%	21.5%	15.3%
$S_{\bar{x}}$		0.9	1.24	0.71	0.57	0.40	0.49

n.s., *, **, not significant a .05 or .01 level respectively.

Appendix 5. Mean squares and levels of significance for dry weight, carbohydrates, and crude protein in both regrowth and roots of tall fescue grown at four temperature regimes.

		Mean Squares and Levels of Significance								
		Regrowth analysis Carbohydrates					Root analysis Carbohydrates			
Sources of variance	d. f.	Dry wt.	% WSC	% fructosans	% free sugars	% C. P.	Dry wt.	% WSC	% fructosans	% free sugars
Cultivar	1	2.00**	67.45*	2.41ns	55.41**	67.77ns	0.236ns	14.78**	5.56**	2.97ns
Temperature	3	11.03**	537.75**	39.33**	312.09**	454.56**	0.959**	23.99**	2.10**	15.45**
Regrowth	1	6.28**	563.47**	85.84**	148.38**	13.27ns	8.592**	48.96**	2.23**	31.27**
Cult. x temp.	3	1.45**	13.86ns	3.34ns	4.78ns	16.74ns	0.472ns	2.90ns	2.02**	1.11ns
Temp. x regr.	3	1.44**	120.30**	10.79*	85.10**	30.78ns	0.436ns	6.92*	0.46ns	4.36*
Cult. x regr.	1	0.40ns	78.10*	8.21ns	38.46**	35.40ns	0.041ns	4.05ns	0.85ns	1.13ns
Cult. x temp. x re.	3	0.17ns	12.85ns	3.40ns	14.58*	17.98ns	0.191ns	1.27ns	0.17ns	1.53ns
Error	48	0.13	10.91	2.58	4.61	23.03	0.205	1.53	0.19	1.22
CV		23.2%	19.8%	46.5%	15.9%	23.2%	26.2%	42.1%	52.8%	51.4%
$S_{\bar{x}}$		0.09	0.83	0.40	0.54	1.20	0.11	0.31	0.11	0.28

n. s., *, **, not significant, significant at .05 and .01 level, respectively.

Appendix 6. Leaf area, tillers per pot and plant, mean relative growth rate, and dry weight of tall fescue grown at four temperature regimes with mean squares and levels of significance.

		Mean Squares and Levels of Significance							
	d.f.	Leaf area (cm^2)	Dry wt./pot	Tillers/pot	Tillers/plant	Leaf area/tiller(cm^2)	Dry wt./tiller (mg)	d.f.	$\overline{RGR}$ (mg/dm)[1/]
Cultivar	1	64,212.17ns	22.87**	297.03ns	6.48ns	11.96ns	1823.85ns	1	3.74ns
Temperature	3	103,145.55**	6.45ns	435.03ns	2.23ns	19.34**	4960.73*	3	260.84ns
Cultivar x temperature	3	22,410.43ns	19.21ns	285.76ns	4.89ns	10.34*	1739.22ns	3	81.83ns
Error	32	18,265.67	2.68	352.89	9.71	3.33	1284.42	72	177.35
CV		35.4%	34.9%	30.6%	25.4%	29.4%	27.1%		36.4%
$S_{\bar{x}}$		27.03	0.16	3.76	0.62	0.37	7.17		1.33

[1/] RGR mg/dry matter/time

n.s., *, **, not significant and significant at .05 and .01 level, respectively.

Appendix 7. Mean squares and levels of significance for perloline and crude protein, and NCE, DR, and gross photosynthesis grown at four temperature regimes for two cultivars of tall fescue.

		Mean Squares and Levels of Significance				($mg\ CO_2 dm^{-2} h^{-1}$)		
Source of variation	d.f.	ug/g perloline	% crude protein	Source of variation	d.f.	NCE	DR	Gross photo.
Cultivar	1	1,392,096.29**	16.21ns	Treat.	7	19.10ns	248.11**	347.76**
Temp.	3	406,103.95**	32.43*	Temp.	3	31.50ns	443.37**	586.05**
Cult. x temp.	3	416,671.91**	18.10ns	Cult.	1	2.81ns	48.51ns	87.64ns
Error	24	11,544.04	12.27	Temp. x cult.	3	12.12ns	151.73**	196.20*
				W/treat.	32	27.07	25.35	46.05
CV		47.5%	6.4%			47.7%	48.4%	31.3%
$S_{\bar{x}}$		26.87	0.27			1.05	1.00	1.36

n.s., *, **, not significant, significant at .05 and .01 level respectively.