Comparative forage yield, water use, and water use efficiency of alfalfa, crested wheatgrass and spring wheat in a semiarid climate in southern Saskatchewan

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Semiarid Prairie Agricultural Research Centre, Agriculture and AgriFood Canada, Box 1030, Swift Current, Saskatchewan, Canada S9H 3X2 (e-mail: JeffersonP@agr.gc.ca). *Received 14 July 2004, accepted 27 April 2005.*

Jefferson, P. G. and Cutforth, H. W. 2005. **Comparative forage yield, water use, and water use efficiency of alfalfa, crested wheatgrass and spring wheat in a semiarid climate in southern Saskatchewan**. Can. J. Plant Sci. **85**: 877–888. Crested wheatgrass (*Agropyron cristatum* L. Gaertn.) and alfalfa (*Medicago sativa* L.) are introduced forage species used for hay and grazing by cattle across western Canada. These species are well adapted to the semiarid region but their long-term responses to water stress have not been previously compared. Two alfalfa cultivars with contrasting root morphology (tap-rooted vs. creeping-rooted) and two crested wheatgrass (CWG) cultivars with different ploidy level (diploid vs. tetraploid) were compared with continuously cropped spring wheat (*Triticum aestivum* L.) for 6 yr at a semiarid location in western Canada. Soil water depletion, forage yield, water use efficiency, leaf water potential, osmotic potential and turgor were compared. There were no consistent differences between cultivars within alfalfa or CWG for variables measured. However, these two species exhibit different water stress response strategies. Leaf water potential of CWG was lower during midday stress period than that of alfalfa or wheat. Alfalfa apparently had greater capacity to osmotically adjust to avoid midday water stress and maintain higher turgor. Soil water use patterns changed as the stands aged. In the initial years of the trial, forage crops used soil water from upper layers of the profile. In later years, soil water was depleted down to 3 m by alfalfa and to 2 m by crested wheatgrass. Alfalfa was able to deplete soil water to lower concentrations than crested wheatgrass or wheat. Soil water depletion by wheat during the non-active growth season (after harvest to fall freeze-up) was much less than for CWG or alfalfa as expected for annual vs. perennial crops. As a result, more soil water was available to wheat during its active growth period. In the last 3 yr, the three species depleted all available soil water. Forage yield responses also changed over time. In the initial 3 yr, crested wheatgrass yielded as much as or more than alfalfa. For the last 3 yr of the experiment, alfalfa yielded more forage than crested wheatgrass. Forage crops deplete much more soil water during periods of aboveground growth dormancy than wheat. Water use efficiency of crested wheatgrass declined with stand age compared with fertilized continuous spring wheat. Alfalfa exhibited deep soil water extraction and apparent osmotic adjustment in response to water stress while CWG exhibited tolerance of low water potential during stress.

Key words: forage yield, soil water, water potential, water use, water use efficiency, drought

Jefferson, P. G. et Cutforth, H. W. 2005. **Comparaison du rendement fourrager, de l'utilisation de l'eau et de l'efficacité de l'utilisation de l'eau chez la luzerne, l'agropyre à crête et le blé de printemps dans une région semi-aride du sud de la Saskatchewan**. Can. J. Plant Sci. **85**: 877–888. L'agropyre à crête (*Agropyron cristatum* L. Gartn.) et la luzerne (*Medicago sativa* L.) sont des espèces fourragères introduites employées pour la production de foin et la paissance des bovins partout dans l'ouest du Canada. Ces espèces se sont bien acclimatées aux conditions semi-arides de la région, mais jamais encore n'a-t-on comparé leur réaction à long terme au stress hydrique. Les auteurs ont comparé deux cultivars de luzerne aux racines de morphologie différente (racines pivotantes ou traçantes) et deux cultivars d'agropyre à crête de ploïdie différente (diploïde et tétraploïde) à la monoculture du blé de printemps (*Triticum aestivum* L.) pendant six ans, dans une région semi-aride de l'Ouest canadien. Les paramètres comparés étaient l'extraction de l'eau du sol, le rendement fourrager, l'efficacité de l'utilisation de l'eau, le potentiel hydrique foliaire, le potentiel osmotique et la turgescence. Les auteurs n'ont relevé aucun écart cohérent entre les cultivars de luzerne et d'agropyre pour les variables examinées. Les deux espèces recourent toutefois à des stratégies différentes pour composer avec le stress hydrique. L'agropyre a un potentiel hydrique foliaire plus faible que celui de la luzerne ou du blé pendant la période de stress du milieu de la journée. Apparemment, la luzerne utilise mieux l'osmose pour éviter le stress hydrique du milieu de la journée et rester turgescente. L'utilisation de l'eau du sol évolue avec l'âge du peuplement. Les premières années de l'expérience, les cultures fourragères utilisaient l'eau présente dans les couches supérieures du profil. Vers la fin du projet, la luzerne avait épuisé l'eau du sol jusqu'à 3 m de profondeur contre 2 m pour l'agropyre à crête. La luzerne extrait plus d'eau du sol que l'agropyre à crête ou le blé. Le blé extrait beaucoup moins d'eau du sol pendant sa période de croissance non active (de la récolte au gel en automne) que l'agropyre à crête ou la luzerne ainsi qu'on pourrait s'y attendre avec des cultures annuelles et vivaces. En conséquence, le blé dispose d'une plus grande quantité d'eau pendant sa période de croissance active. Au cours des trois dernières années, les trois espèces ont épuisé toute l'eau présente dans le sol. Le rendement fourrager a lui aussi évolué dans le temps. Au cours des trois premières années, l'agropyre à crête avait un rendement identique ou supérieur à celui de la luzerne. Lors des trois dernières cependant, le rendement de la luzerne dépassait celui de l'agropyre. Les cultures fourragères extraient beaucoup plus d'eau du sol que le blé pendant la période de dormance des organes aériens. L'efficacité avec laquelle l'agropyre utilise l'eau diminue avec l'âge du peuplement comparativement au blé de printemps cultivé continuellement avec fertilisation. La luzerne extrait l'eau du sol en profondeur et procède apparemment à un ajustement osmotique quand l'eau vient à manquer alors que l'agropyre à crête tolère la réduction du potentiel hydrique en période de stress.

Mots clés: Rendement fourrager, eau du sol, potentiel hydrique, utilisation de l'eau, efficacité de l'utilisation de l'eau, sécheresse

Abbreviations: **CWG**, crested wheatgrass; **DM**, dry matter; **WUE**, water use efficiency; $\Psi_{\mathbf{pd}}$, predawn leaf water potential; $\Psi_{\mathbf{md}}$, midday leaf water potential; $P_{\mathbf{pd}}$, predawn turgor; $P_{\mathbf{md}}$, midday turgor; $\pi_{\mathbf{pd}}$, predawn osmotic potential; $\pi_{\mathbf{md}}$, midday osmotic potential

Crested wheatgrass (CWG) (*Agropyron cristatum* L. Gaertn.) has been seeded across the prairie region of western Canada since the 1930s (Gray 1996) and used for hay and spring grazing by beef cattle. It establishes quickly, excludes weedy competitors, and complements native rangeland by providing sustainable forage production during the spring and fall (Knowles and Kilcher 1983). Forage production is correlated to precipitation but this relationship changes as the CWG stands age over the first 3 yr (White 1985). Thirty-five-year-old stands of CWG were stable communities with 90% of plant biomass produced by CWG and only 10% by native plants (Looman and Heinrichs 1973). These authors concluded that CWG is a long-term replacement for native range for sustainable forage production. In a recent report, Campbell et al. (2000) reported that CWG in a long-term crop rotation experiment exhibited a decline in forage production after 5 yr compared with continuous spring wheat rotation. These results suggested that CWG forage production may not be as sustainable over time as Looman and Heinrichs (1973) had concluded.

Diploid CWG (A. *cristatum*) ($2N = 2\times = 14$) is commonly grown in western Canada while tetraploid CWG (A. *desertorum*) ($2N = 4\times = 28$) is more commonly grown in the United States of America because the tetraploids are more drought tolerant (Bruynooghe 1996). Kirk CWG is a natural tetraploid cultivar of A. *cristatum* that exhibits improved forage production in western Canada over diploid cultivars (Knowles 1990). However, its adaptation to water stress was not known.

Forage yield and quality of CWG can be improved by seeding with alfalfa (*Medicago sativa* L.). Alfalfa roots extract soil moisture below 1.5 MPa tension, which is normally assumed to be the lower limit of available water to crop plants (Cutforth et al. 1991). This drying of the soil profile was greater with older alfalfa stands. Jefferson and Cutforth (1997) reported that alfalfa yield was less dependent on precipitation in the first 2 yr after establishment, likely because the plants were exploiting stored soil water. They suggested that soil water depletion should be measured in dryland alfalfa stands to account for alfalfa's apparent drought tolerance. There has been confusion about the impact of alfalfa root morphology on its capabilities for soil water extraction. For example, Henry et al. (1987) describe alfalfa as exhibiting a tap root that can reduce excess soil water that contributes to salinization of prairie soils. However, in a table of recommended forage species for seeding on saline soils, these same authors recommend Rambler alfalfa, a creeping-rooted cultivar. Creeping-rooted cultivars were developed for persistence, particularly under grazing (Heinrichs 1963), and we were not aware of any research on the impact this trait might have on soil water use.

A summary of reported alfalfa water use efficiency (WUE) from eight locations in the USA indicated that it produces 15.2 ± 2.1 kg ha^{-1} mm^{-1} (Sheaffer et al. 1988). In California, irrigated alfalfa WUE was reported to be 23.2 kg ha^{-1} mm^{-1} (Grimes et al. 1992). Dryland alfalfa WUE has not been reported for semiarid conditions in western Canada. Several water use and long-term crop production studies at Swift Current, Saskatchewan have studied spring wheat (*Triticum aestivum* L.) (Campbell et al. 1987, 1988). We used this common annual crop for comparison to perennial forage crops and to provide a benchmark that can be readily compared with previous results.

The objective of this work was to compare spring wheat, two cultivars of CWG, and two alfalfa cultivars for forage production, water use, water use efficiency, and plant water status in a long-term experiment at Swift Current, Saskatchewan.

MATERIALS AND METHODS

An experiment was conducted at Swift Current, Saskatchewan (50°16′N 107°44′W, elev. 825 m) on a Brown Chernozem Swinton loam soil (Agriculture Canada Expert Committee on Soil Survey 1987) from 1993 to 1998. Two CWG cultivars, Kirk (Knowles 1990) and Parkway (Alderson and Sharp 1994), two alfalfa cultivars, Beaver (Bolton et al. 1963) and Rangelander (Heinrichs et al. 1979) were compared with continuous spring wheat. These two alfalfa cultivars remain popular with local producers despite their age. They represent contrasting root morphology as Beaver exhibits a tap-root architecture while Rangelander is predominantly (80%) creeping-rooted (Heinrichs et al. 1979). The experimental design was a randomized complete block of five treatments with nine replications. The replications were grouped three per range (oriented east–west) on three ranges stacked south to north. The individual plots were 12 seeded rows spaced 0.3 m apart for plot dimensions of 3.6 × 36 m. CWG and alfalfa were seeded on 1992 May 25 at 6 and 4 kg ha^{-1}, respectively. Annual weeds were controlled by clipping during 1992 and no data were recorded during the establishment of perennial forage plots.

The site was irrigated during the spring of 1993 to raise the soil water concentration to field capacity to a depth of 3 m prior to seeding wheat. A total of 175 mm of irrigation water was applied during a 7 d period. Irrigation ensured that the soil water concentration was as uniform as possible in order to compare water depletion by depth as suggested for alfalfa by Jefferson and Cutforth (1997). A 21-mo fallow period at this location can store an additional 96 mm of soil water in dryland rotations (Campbell et al. 1987) while irrigated alfalfa typically requires about 400 mm of irrigation water at this location (Pohjakas et al. 1967). So we concluded that the irrigation water provided only in 1993 to permit root exploration of the soil profile did not invalidate the characterization of this trial as dryland.

This irrigation resulted in a delay of spring growth by the alfalfa and CWG and a delay in seeding the spring wheat in 1993 (Table 1). Spring wheat was no-till seeded at recommended rates (Table 1) on the same plots year after year and fertilized with N at 80 kg ha^{-1} and P_2O_5 at 31 kg ha^{-1}, while alfalfa and CWG were not fertilized because this is the typical agronomic practice of forage producers in this region. The wheat cultivar was Leader in 1993 and 1994 but this was changed to Lancer from 1995 to 1998. Lancer has greater genetic resistance to wheat stem sawfly (*Cephus cinctus)*, a common problem on continuous wheat crops in this region. Weeds were controlled in the spring wheat with post-emer-

Table 1. Dates of seeding and harvest for continuous wheat, dates of spring growth initiation, fall freeze-up, and harvest on forage crops, dates of water potential sampling, and total growing season (April to August) precipitation for 6 yr

	1993	1994	1995	1996	1997	1998
Wheat seeding date	Jun. 09	Apr. 29	May 09	May 23	May 14	May 13
Wheat harvest date	Sep. 08	Aug. 22	Aug. 22	Aug. 29	Aug. 21	Sep. 03
Forage spring green date	May 28	Apr. 11	Apr. 12	Apr. 17	Apr. 30	Apr. 08
Forage harvest date	Aug. 09	Jun. 28	Jul. 06	Jun. 27	Jul. 11 21 Aug.	Jul. 08
Fall freeze-up date[z]	Oct. 19	Oct. 19	Oct. 16	Oct. 16	Oct. 27	Sep.03[x]
Water potential sampling dates	None	May 18 Jun. 01 Jun. 15 Jun. 30 Jul. 13 Jul. 27 Aug. 10 Aug. 24	May 18 Jun. 01 Jun. 14 Jun. 28 Jul. 12 Jul. 26 Aug. 22	May 29 Jun. 12 Jun. 26 Jul. 10 Jul. 24 Aug. 08	Jun. 02 Jun. 17 Jul. 01 Jul. 15 Jul. 28 Aug. 11	May 26 Jun. 04 Jun. 23 Jul. 07 Jul. 21 Aug. 11

[z] Last date of soil water monitoring after a –5°C frost.

[x] Termination date of experiment.

gence herbicide application. In 1992, aluminum access tubes were installed to 3-m depth in the centre of each plot. Volumetric soil water was determined by neutron probe at 10, 30, 50, 70, 90, 110, 130, 150, 170, 190, 210, 230, 250 and 270 cm depths at spring greening, forage harvest, wheat harvest, and freeze-up in the fall to track soil water use by the plants. Available soil water (field capacity minus permanent wilting point) is 268 mm in this soil. Non-growing season water use was summed from harvest date to fall freeze-up. Daily rainfall and Class-A pan evaporation were recorded at an automated weather station located 200 m from the experiment. Water use (rainfall plus soil water depletion) was summed from spring green-up to fall freeze-up for all three crops. Growing season water use was summed from seeding to grain harvest date for wheat or from spring green-up to forage harvest date for alfalfa and CWG.

Two leaves were sampled on plants adjacent to neutron access tubes for replications 3, 4, and 5 at several dates each season for determination of plant water status from 1994 to1998 (Table 1). The youngest, fully expanded leaf of CWG or wheat or the youngest, fully expanded trifoliate leaf of alfalfa were excised with a razor blade and placed in a plastic bag to minimize water loss (Turner and Long 1980). The leaf was then placed in a pressure chamber apparatus (PMS Instrument Co., Corvallis, OR) with the cut end exposed. The chamber was pressurized with N_2 gas until water extruded from xylem vessels when viewed with a 10× binocular microscope mounted above the chamber. Leaf water potential (Ψ) was determined at pre-dawn (Ψ_{pd}) and midday (Ψ_{md}) periods, which represent minimum and maximum diurnal water stress. At the same time, leaf tissue of the same age and orientation was excised and placed in 5-mL plastic syringes with a small amount of glass wool in the tip end. These syringes were placed in a freezer to rupture the cell membranes of the leaves. Within 3 mo, these samples were thawed and the plant material manually pressurized with the plunger to exude sap (cell solubles and apoplastic water) on to filter paper disks. The osmotic potential (π) was determined with a Vapour Pressure Osmometer (Model 5500XR, Wescor, Logan, UT) without correction for apoplastic water dilution of cell solubles. Turgor (P) was determined from the components of water potential (Ψ) within plant tissues (Fitter and Hay 1983):

$$\Psi = \mathrm{P} - \pi \qquad (1)$$

where π is osmotic potential and P is turgor. The water potential component for gravity was negligible (<0.01 MPa) (Fitter and Hay 1983). Negative turgor values were obtained by calculation of P but this reflected an underestimation of π due to dilution of cell sap by apoplastic (cell wall) water (Campbell et al. 1979). We report the negative P values but recognize that negative turgor does not occur in nature. Water potential, osmotic potential and turgor readings from both predawn and midday samples were analyzed by date within each year.

Forage yield of CWG was determined in late June or early July of each year (Table 1) by harvesting 0.6 × 36 m area of each plot with a flail plot harvester and recording the fresh forage mass. A 300-g subsample was weighed, dried in a forced-air oven at 60°C for 48 h and reweighed to determine dry matter (DM) concentration. Forage DM yield was calculated for each plot. Regrowth in 1997 was sufficient for a second harvest for alfalfa (Table 1) but not for CWG. Biomass yield (grain, chaff, and straw) of wheat was determined at the time of grain yield harvest. In 1994 and 1997 wheat biomass yield data were lost so biomass yield of wheat was derived by calculation based on grain yield and harvest index for each plot.

Water use efficiency was derived by dividing forage DM yield by water use (Eq. 2) from spring green-up to fall freeze-up, similar to the season-long approach of Scheaffer et al. (1988). No attempt was made to separate soil water depletion into evaporation and transpiration components.

$$\mathrm{WUE\ (kg\ ha^{-1}\ mm^{-1}) = forage\ DM\ yield\ (kg\ ha^{-1})} \div \mathrm{water\ use\ (mm)} \qquad (2)$$

We considered the Campbell et al. (1988) approach to calculate soil water use by wheat from seeding to harvest plus growing season precipitation. This would have created a confounding factor in our calculations, however, because the spring wheat would have a different period of water use than CWG or alfalfa. Our approach to calculating WUE includes soil water use by the perennial crops during periods of aboveground growth dormancy, such as during late summer and in the autumn, because this water use is important for maintaining crown and root tissues and carbon reserves for regrowth initiation. Restricting WUE calculation to water used only during the period of active aboveground growth would over-estimate WUE of perennial crops. We concluded that the water use from green-up to fall freeze-up would be the best period for comparison between annual and perennial crops.

Analysis of variance based on a two-factor [replication (n = 9), crop (n = 5)] model was calculated for each year or sampling date with JMP software (SAS Institute, Inc.1995). Analysis of variance in JMP is based on the General Linear Model of SAS and least square means were generated. Contrasts were calculated to compare: forage crops vs. spring wheat, CWG vs. alfalfa, Rangelander vs. Beaver alfalfa, and Kirk vs. Parkway CWG.

RESULTS AND DISCUSSION

Water Use

From green-up to freeze-up, differences between species in water use (WU) occurred during the first 3 yr of the study (Table 2). There were no differences in WU between cultivars within alfalfa or CWG (data not shown). Therefore, amounts and patterns of WU for a given species were determined by averaging across cultivars within species. Alfalfa used more water than CWG in 1994 and 1995 and more water than wheat in 1993 and 1995. There were no differences between species in WU from 1996 to 1998, although alfalfa tended to use more water than CWG or wheat. CWG used more water than wheat only in 1993. Because the time periods from green-up and freeze-up were the same for both perennial species, water use per day (WU d^{-1}) followed the same significance and trends as WU.

Because the duration of the growing season (growth period over which machine-harvestable dry matter was produced) was 19 or more days longer for wheat compared with alfalfa and CWG, wheat used more water during the growing season than alfalfa and CWG (Table 2). Except for 1993 and 1996, alfalfa used more water during the growing season than CWG. The opposite occurred for WU d^{-1}. During 1993 and 1994 WU d^{-1} was higher for alfalfa and CWG compared with wheat. Thereafter, WU d^{-1} was highest for wheat. Alfalfa and CWG were not fertilized, but wheat was fertilized. During 1993 and 1994, fertility and water were sufficient to support good growth of all three species. Thus, despite the much shorter growing season, WU for alfalfa and CWG was only slightly less than and WU d^{-1} slightly greater than for wheat. The growth of alfalfa and CWG decreased substantially compared with wheat in the last 3 yr, resulting in wheat using more water and having higher daily water use compared with alfalfa and CWG. This decline in growth may be related to the decline in natural soil fertility as the stands aged.

The duration of the non-growing season was much longer for alfalfa and CWG than for wheat (Table 2). Partly because of the longer duration, WU during the non-growing season was much greater for alfalfa and CWG compared with wheat. The differences in non-growing season WU were so large that, despite the longer durations, WU d^{-1} was larger for alfalfa and CWG compared with wheat. In general, there were no differences in WU and WU d^{-1} between alfalfa and CWG.

The WU of irrigated alfalfa at this site was 637 mm (Pohjakas et al. 1967), including 400 mm of irrigation water. Irrigated spring wheat used 526 mm of soil water and irrigation over the whole season (Pohjakas et al. 1967). In comparison, dryland alfalfa in our experiment used an average of 414 mm and wheat used an average of 387 mm of soil water. Our data suggest that perennial forage crops will use re-charge soil water as effectively as an annual crop such as wheat and can also exploit soil water stored in deeper soil layers than wheat.

Precipitation received from fall freeze-up to seeding for wheat or to spring green-up for CWG and alfalfa varied among years (Table 3), reflecting the different growth periods for these species. Over-winter precipitation was lowest for the 1998 season and was highest for 1996 (wheat) or 1997 (CWG and alfalfa). Wheat benefitted from precipitation received from harvest to freeze-up, which contributed to soil water recharge. This was accounted for in water use efficiency calculations as the additional soil water would be measured in the spring of the next year. For alfalfa and grass, a large proportion of the forage harvest to freeze-up precipitation would be transpired as the plants are still living, and this transpired water would, therefore, be lost from the soil profile and unavailable for biomass production the following year. However, photosynthesis during the aboveground growth dormancy period likely contributed to root energy reserves that are essential to regrowth in the next spring. Approximately 25% more rainfall occurred during the growing season for wheat (seeding to harvest) than for alfalfa or grass (green-up to harvest).

Evaporation indicated that alfalfa and CWG experienced water stress in 1993 and moist conditions in 1996 (Table 3). Wheat experienced water stress in 1998.

Soil Water Depletion

From 1993 to 1995, alfalfa depleted more water than CWG and wheat from lower depths (Fig. 1). For example, alfalfa depleted more water than wheat from the surface to 1.3-m layer in 1993, and more water than wheat and CWG from the 1.3-m to 2.1-m layer in 1994, and from the 1.7-m to 2.3-m layer in 1995. From 1996 to 1998, in general, alfalfa depleted more water than CWG and wheat from below 1.7 m. Generally, throughout the 6 yr of the study, alfalfa tended to deplete more water than CWG and wheat from below 1.5 m. Only in 1993 did CWG deplete more water than wheat to 1.3 m, whereas the reverse occurred in 1994. Thereafter, CWG and wheat depleted similar amounts of water to 1.3 m. In most years CWG and wheat depleted similar amounts of water from the 1.3-m to 2.1-m layer except in 1994 when CWG depleted more water from 1.5- and 1.7-m depths than wheat.

The species-dependent water use patterns were a reflection of the rooting depth differences between species. Our soil water depletion data suggested that the maximum root-

Table 2. Duration (d) and water use (WU) and water use per day (WU d^{-1}) by alfalfa, crested wheatgrass (CWG) and spring wheat from green-up to freeze-up, and for the growing season and for the non-growing season when no harvestable dry matter was produced

		Green-up to freeze-up			Growing season			Non-growing season		
Year	Crop	Days	WU (mm)	WU d^{-1}	Days	WU (mm)	WU d^{-1}	Days	WU (mm)	WU d^{-1}
1993	Alfalfa	145	450	3.1	73	311	4.3	72	139	1.9
	CWG	145	433	3.0	73	298	4.1	72	135	1.8
	Wheat	145	389	2.7	92	346	3.8	53	42	1.0
	SE[z]		22**	0.2**		23**	0.3**		20**	0.3**
1994	Alfalfa	192	453	2.4	79	306	3.9	113	148	1.3
	CWG	192	424	2.2	79	290	3.7	113	134	1.2
	Wheat	192	440	2.3	116	366	3.2	76	74	0.9
	SE		19*	0.1*		14**	0.2**		14**	0.1**
1995	Alfalfa	183	467	2.6	86	149	1.7	97	318	3.3
	CWG	183	406	2.2	86	126	1.6	97	280	2.9
	Wheat	183	405	2.2	106	308	3.0	77	97	1.2
	SE		18**	0.1**		13**	0.1**		12**	0.2**
1996	Alfalfa	184	432	2.3	72	163	2.3	112	269	2.4
	CWG	184	413	2.2	72	141	2.0	112	273	2.5
	Wheat	184	416	2.3	99	362	3.7	85	54	0.6
	SE		NS	NS		23**	0.3**		19**	0.2**
1997	Alfalfa	181	408	2.3	72	234	3.3	109	174	1.6
	CWG	181	385	2.1	72	199	2.8	109	186	1.7
	Wheat	181	405	2.2	99	299	3.0	81	107	1.2
	SE		NS	NS		19**	0.2**		20**	0.2**
1998	Alfalfa	121	274	2.3	64	123	1.9	57	151	2.7
	CWG	121	269	2.2	64	105	1.6	57	164	2.9
	Wheat	121	269	2.2	114	257	2.3	7	12	1.2
	SE		NS	NS		14**	0.2**	14*		0.4*

[z]SE is the standard error.

*, ** significantly different at $P < 0.05$, and $P < 0.01$, respectively; NS, non-significant at $P = 0.05$.

Table 3. Precipitation and evaporation (Class A pan) totals for the time periods indicated. In 1993, the study started on May 28, shortly after the soil profile had been filled to field capacity to 3 m by irrigation. The study ended on 8 September 1998, the day spring wheat was harvested. Therefore, freeze-up' in 1998 was Sep. 08

	Wheat			Alfalfa/crested wheatgrass			
Year	Freeze-up to seeding	seeding to harvest	harvest to freeze-up	Freeze-up to green-up	green-up to 1st cut	1st cut to 2nd cut	1st/2nd cut to freeze-up
				Precipitation (mm)			
1993	–	314	60	–	173	–	210
1994	104	173	62	94	146	–	99
1995	99	261	104	74	176	–	213
1996	196	139	112	117	158	–	168
1997	174	199	45	172	148	53	45
1998	57	200	–	43	170	–	44
				Evaporation (mm)			
1993	–	617	97	–	710	–	92
1994	NA	662	251	NA	400	–	728
1995	38	742	208	NA	452	–	536
1996	99	719	155	NA	289	–	696
1997	106	766	315	NA	540	333	315
1998	110	959	–	NA	494	–	574

NA not available due to low temperature.

ing depth for wheat was about 1.5 m, about 2.3 m for CWG, and >2.7 m (probably at least 3 m) for alfalfa. Campbell et al. (1988) also reported water use by spring wheat to 1.5 m depth. In contrast to our results, Bittman (1985) reported soil water depletion by CWG ranged from 0.8 to 1.2 m depth at Melfort, Saskatchewan.

Freeze-up Soil Water Content

The differences between species in freeze-up soil water content with depth reflects the species differences in soil water use patterns (Fig. 2). As the years progressed, the thickness of the soil layer where alfalfa had a lower soil water content at freeze-up compared with CWG increased and moved

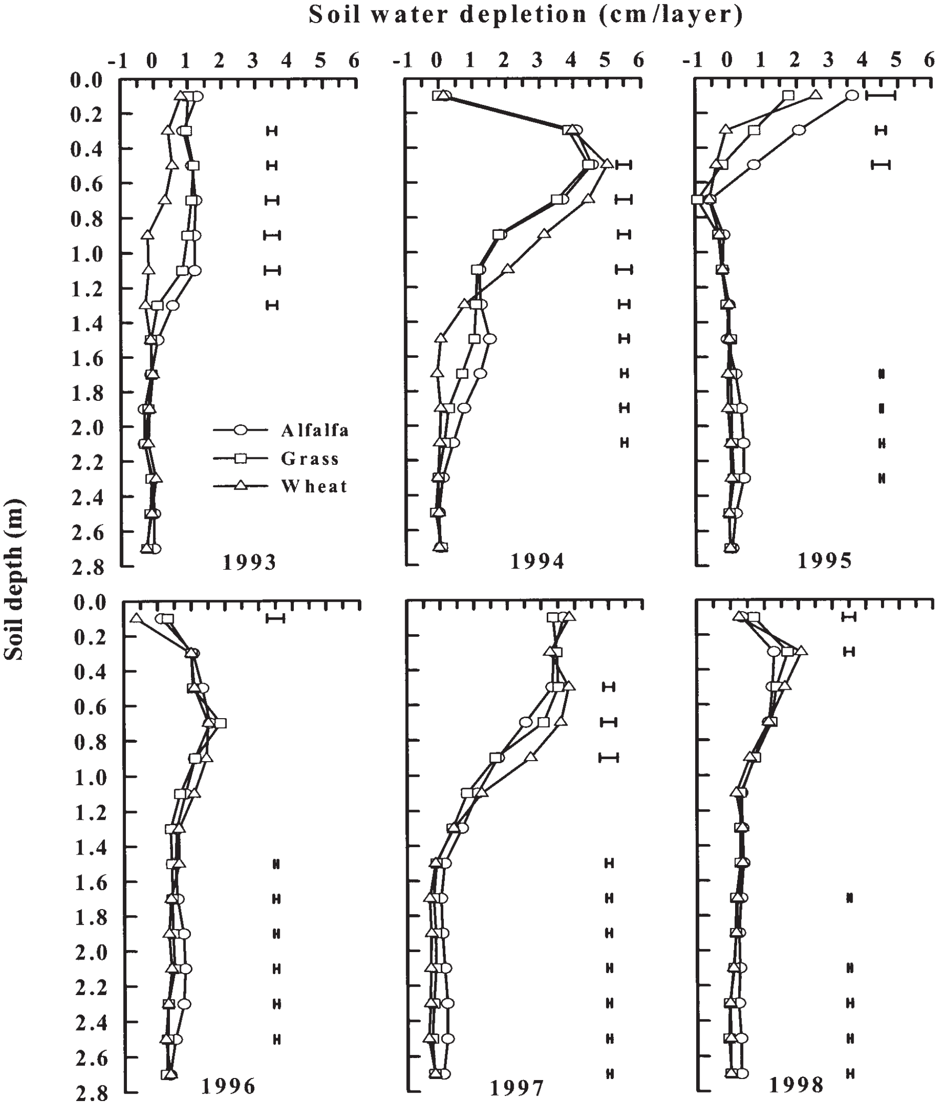

Fig. 1. Annual soil water depletion curves to 2.8 m for alfalfa, crested wheatgrass and spring wheat from 1993 to 1998. LSD bars ($P < 0.05$) at a given depth are for comparing means among species.

downward. For example, in 1993, alfalfa had a lower soil water content than CWG from 1.1 m to 1.5 m, but the thickness of this layer increased to 1.1 m to 2.1 m in 1994, and to 0.3 m to 2.3 m in 1995. As the upper portion of the soil profile dried, alfalfa used more water at deeper depths so that by 1997 and 1998, alfalfa had the lowest soil water content at the deeper depths compared with CWG and wheat.

Even though for any given year CWG did not deplete significantly more water than wheat from below 1.3 m (Fig. 1), CWG tended to deplete more water than wheat from the 1.3-m to 2.1-m layer. Therefore, the freeze-up soil water content from 1.3 m to 2.1 m was significantly lower for CWG compared with wheat from the beginning to the end of the study (Fig. 2).

By 1997, all three species had used similar amounts of water from the surface to 0.9-m depth so there were no differences between species in soil water to 0.9 m (Fig. 2). There were differences in soil water content below 0.9 m with alfalfa having the lowest soil water content below 0.9 m, and with CWG having a lower soil water content than wheat from 1.3 m to 2.1 m.

Forage Yield

Forage yield comparisons among the crops changed with time. In 1993, CWG yielded more than alfalfa, which produced more than spring wheat (Table 4). In 1994, alfalfa yielded more than CWG while spring wheat was intermediate. From 1995 to 1998, spring wheat biomass yield was greater than alfalfa forage yield, except in 1997 when they were similar. During 1994 to 1998, CWG was the lowest-yielding species. Looman and Heinrichs (1973) reported

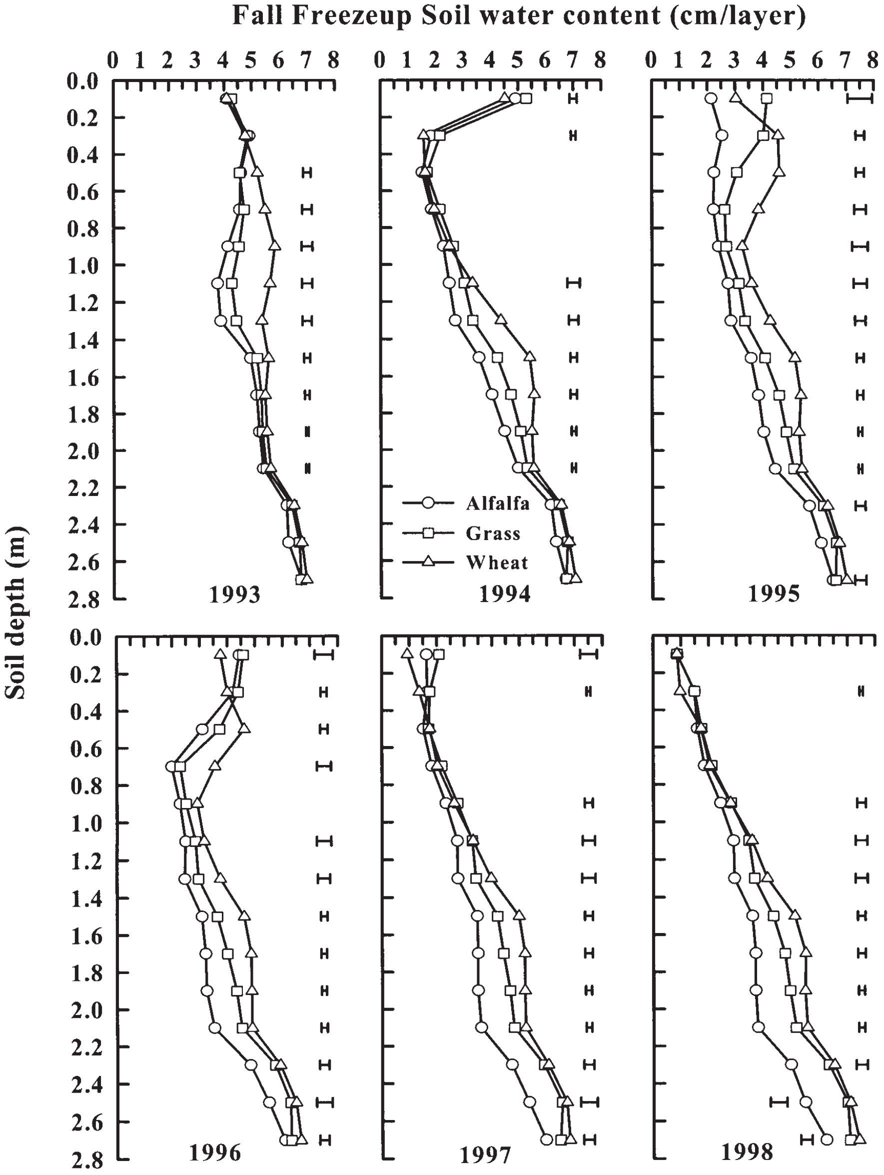

Fig. 2. Fall freeze-up soil profile water content to 2.8 m for alfalfa, crested wheatgrass, and spring wheat from 1993 to 1998. LSD bars ($P < 0.05$) at a given depth are for comparing means among species.

that CWG forage yield stabilized at a low level over time, but we did not observe this trend in our results. There were no differences between Kirk and Parkway CWG or between Rangelander and Beaver alfalfa for forage yield.

Forage yield at this location is correlated to growing season precipitation but newly seeded forage stands may be less dependent on precipitation while depleting soil water from deeper layers (Jefferson and Cutforth 1997). Forage producers in this region generally recognize the higher productivity of newly seeded stands and adjust their management by preferentially haying younger stands and deferring haying or grazing of older stands during “wet” growing seasons.

WUE

As previously observed for forage yield, WUE differences changed with time (Table 5). In 1993, CWG exhibited the highest WUE, while spring wheat had the lowest. The WUE values for CWG in 1993 were similar to those reported for this species in 1984 at Melfort, Saskatchewan (Bittman 1985). In 1994, alfalfa exhibited the highest WUE while CWG had the lowest. In 1995, there were no crop species differences in WUE, but from 1996 to 1998, alfalfa had the highest and CWG had the lowest WUE. There was a significant negative correlation between time (age of stand in years) and WUE in CWG ($r = -0.89$, $n = 6$, $P = 0.05$). White (1985) reported a curvilinear response in CWG between age

Table 4. Forage yield of crested wheatgrass and alfalfa and biomass of continuous spring wheat grown on dryland for 6 yr at Swift Current, Saskatchewan

Crop	Cultivar	1993	1994	1995	1996	1997	1998	6-yr mean
					(Mg ha^{-1})			
CWG	Kirk	8.71	3.49	2.42	1.94	2.92	0.77	3.38
	Parkway	9.47	4.27	2.37	1.82	2.50	0.56	3.50
Alfalfa	Beaver	8.08	6.33	3.13	3.79	5.43	2.01	4.80
	Rangelander	8.29	6.20	3.23	4.01	5.89	1.94	4.93
Spring wheat		7.14	5.50	6.48	5.03	4.87	2.37	4.93
Contrast pobabilities								
Wheat vs. CWG & Alfalfa		<0.01	NS	<0.01	<0.01	0.03	<0.01	<0.01
CWG vs. Alfalfa		0.02	<0.01	<0.01	<0.01	<0.01	<0.01	<0.01
Kirk vs. Parkway		NS	0.07	NS	NS	NS	0.08	NS
Beaver vs. Rangelander		NS	NS	NS	NS	NS	NS	NS
SE		1.12	0.90	0.67	0.43	0.83	0.25	0.35

Table 5. Water use efficiency (WUE) of crested wheatgrass, alfalfa, and continuous spring grown for 6 yr at Swift Current, Saskatchewan

Crop	Cultivar	1993	1994	1995	1996	1997	1998	6 year mean
					kg ha^{-1} mm^{-1}			
CWG	Kirk	28	12	20	11	8	5	14
	Parkway	32	14	19	11	6	2	14
Alfalfa	Beaver	26	22	22	23	15	16	21
	Rangelander	26	20	22	24	16	18	21
Spring wheat		20	15	23	11	14	8	15
Contrast probabilities								
Wheat vs. CWG & Alfalfa		<0.01	0.09	NS	<0.01	<0.01	0.06	<0.01
CWG vs. Alfalfa		0.01	<0.01	0.08	<0.01	<0.01	<0.01	<0.01
Kirk vs. Parkway		0.08	NS	NS	NS	NS	0.08	NS
Beaver vs. Rangelander		NS	NS	NS	NS	NS	NS	NS
SE		4	4	4	4	2	3	2

of stand and WUE and argued that CWG yield and WUE stabilized 3 yr after establishment. We did not observe this response as WUE appeared to decline linearly with age of stand in this study. White (1985) used only seasonal precipitation and did not measure soil water depletion in his calculation of WUE. So his values may differ from ours because we accounted for soil water depletion. The alfalfa WUE values in 1997 (Table 5) were similar to those reported by Sheaffer et al. (1988), while values from 1994 to 1996 were similar to those reported by Grimes et al. (1992). As with forage yield and WU, there were no cultivar differences for WUE between Kirk and Parkway CWG or between Beaver and Rangelander alfalfa (Table 5). The creeping-rooted trait in Rangelander alfalfa was selected to impart persistence and tolerance to grazing (Heinrichs 1963) and did not exhibit improved soil water uptake characteristics or WUE compared with tap-rooted Beaver alfalfa. Tetraploid and diploid Russian wildrye [*Psathyrostachys juncea* (Fisch.) Nevski] had similar WUE at a site in North Dakota (Frank and Berdahl 1999). Our results suggest that the reported yield advantage of tetraploid A. *desertorum* cultivars over diploid A. *cristatum* (Bruynooghe 1996) cultivars in semiarid environments may be due to traits other than ploidy level.

The WUE of continuous spring wheat in this study was similar to previous reports by Campbell et al. (1987). Those authors reported considerable variation in WUE over 18 yr of fertilized continuous spring wheat rotation, so the year-to-year variation in our 6-yr study was not surprising. The most interesting result of our study was alfalfa's superior WUE compared with CWG or continuous wheat, particularly in the last 3 yr (1996 to 1998). Alfalfa is frequently grown under irrigation in North America and is known to respond to supplementary water application (Sheaffer et al. 1988). These results clearly show that dryland alfalfa has WUE superior to either CWG or continuous wheat. This observation leads us to speculate that biological N fixation in alfalfa may contribute to improved WUE by reducing N limitation to growth under water-limiting conditions. However, CWG experienced both water- and N-limiting conditions. While we did not examine the impact of fertility on WUE of CWG, we speculate that additional fertility would improve it. Producers in this region argue that large annual variation in precipitation makes fertilization of perennial forages uneconomical. If long-range weather predictions could be made more accurately in the future, then this agronomic practice should be re-evaluated.

Water Potential

Midday water potential (Ψ_{md}) over the growing season exhibited different responses related to the weather and potential water stress. For example, Ψ_{md} declined during the

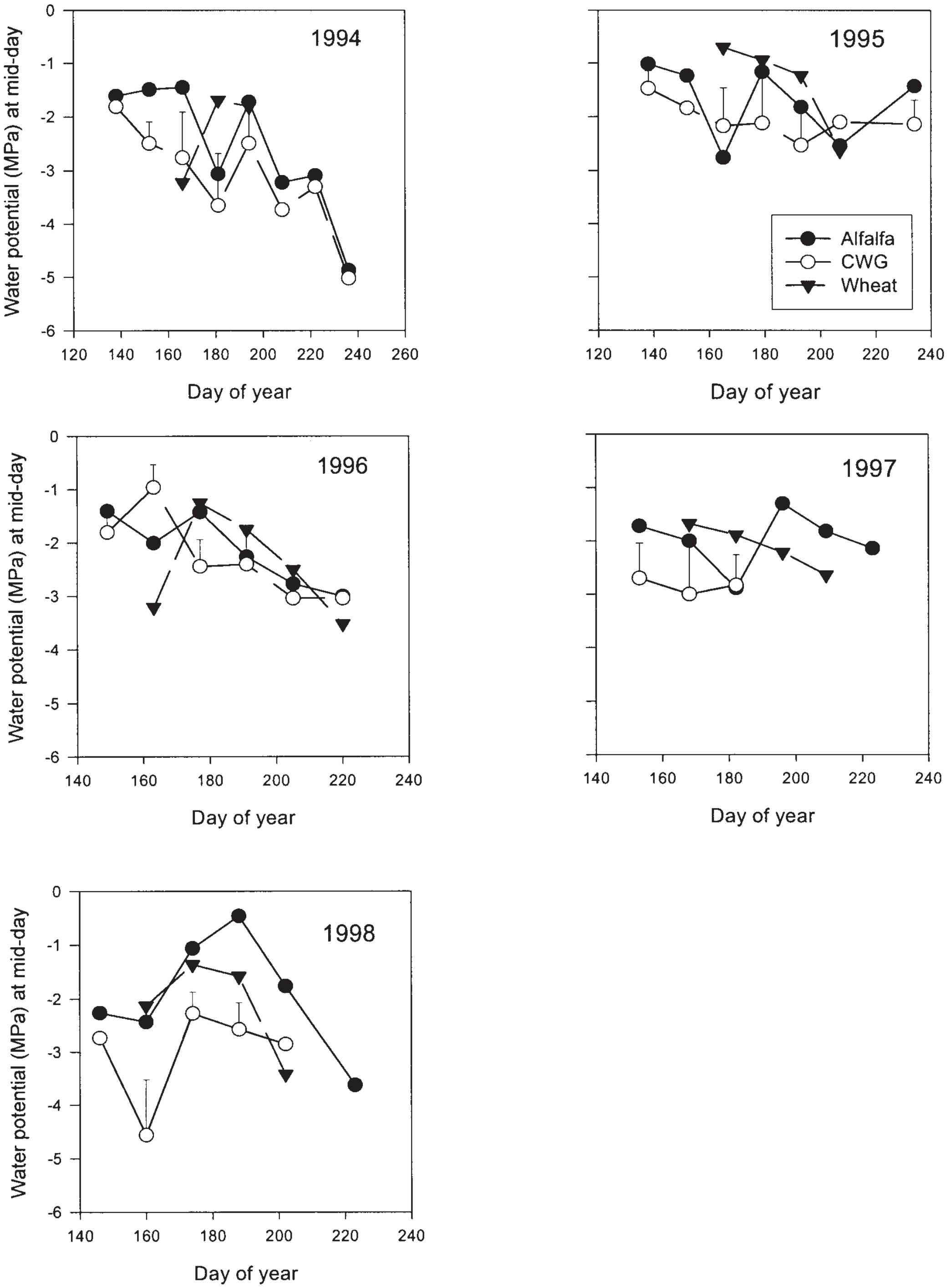

Fig. 3. Mid-day leaf water potential for three crop species in each of 5 yr at Swift Current, Saskatchewan. Vertical bars indicate LSD value among means on sampling dates where crops were significantly different.

summer season in 1994 but it declined much less in 1996 (Fig. 3). This was consistent with evaporation potential differences between these two seasons (Table 3).

There were no consistent differences between Rangelander and Beaver alfalfa cultivars or between Kirk and Parkway CWG cultivars. The contrasts for CWG or for alfalfa cultivars were significant only twice for Ψ in each species. Therefore, we present species means of all sampling dates within each year to illustrate species comparisons.

Mean predawn water potential (Ψ_{pd}) over all dates within a year did not differ among the crops except in 1998 (Fig. 4A).

In 1998, alfalfa and CWG had lower Ψ_{pd} values than wheat. The Ψ_{pd} values from 1994 to 1997 suggest that all three species began each sampling day with similar water status.

The Ψ_{md} differed among the crops in each year (Fig. 4B). In 1994 and 1995, CWG exhibited the lowest Ψ_{md} values and wheat the highest. In 1994, CWG leaves experienced –3.0 MPa water potential, a value that indicated severe water stress. In 1996, both CWG and wheat had lower water potentials than alfalfa. In 1997 and 1998, CWG had the lowest Ψ_{md} values while alfalfa and wheat were similar. Overall, CWG experienced the lowest water potentials or the highest degree of water stress among the three species. This suggests that CWG exhibits a different strategy to cope with water stress than alfalfa or wheat. Alfalfa and wheat maintain high water potential in their tissues in order to avoid stress (Fitter and Hay 1983) but CWG tolerates very low Ψ_{md} within its leaf tissues during the mid-day period of water stress (Fig. 4B) and then recovers to water potential values similar to alfalfa and wheat at night (Fig. 4A). These Ψ_{md} values for CWG are similar to drought-stressed values reported by Bittman and Simpson (1989). They found that CWG Ψ_{md} values were lower than those of Altai wildrye [*Leymus angustus* (Trin.) Pilger] or smooth bromegrass (*Bromus inermis* Leyss.) at a site in northeastern Saskatchewan. They also reported that CWG exhibited leaf rolling under water stress (Bittman and Simpson 1989) as a strategy to reduce transpirational water loss from adaxial leaf stomata and radiation interception by reducing leaf area. We did not rate leaf rolling in our study but it was observed within the CWG plots.

Predawn osmotic potential (π_{pd}) differed among the crops in every year (Fig. 5A). Wheat consistently had the highest (least negative) π_{pd} values in every year. Alfalfa and CWG had similar π_{pd} values in every year except 1997 when alfalfa was lower than CWG. Midday osmotic potentials (π_{md}) varied among crops in every year except 1995 (Fig. 5B). As with π_{pd} observations, π_{md} was higher for wheat in every year. CWG and alfalfa had similar π_{md} in most years.

Predawn turgor (P_{pd}) differed among the crops in 1995, 1996 and 1998 (Fig. 6A). In those 3 yr, either alfalfa or CWG had the highest P_{pd} while wheat had the lowest in 2 of 3 yr. Midday turgor (P_{md}) varied among the crops in all 5 yr (Fig. 6B). CWG had the lowest P_{md} in 4 out of 5 yr, while alfalfa had the highest P_{md} in 1994, 1996, 1997 and 1998. High P_{md} would permit continued carbon assimilation, cell extension, and growth during the period of water stress. Alfalfa maintains high turgor during low water stress periods at predawn, and during high water stress periods during the day. This is a very different strategy compared with CWG, which allows very low Ψ_{md} and P_{md} values to occur in its tissues. CWG does not appear to adjust to water stress through the active accumulation of osmotic solutes. Rather through an elastic cell wall, CWG tolerates low Ψ_{md} and exhibits other water-conserving strategies such as leaf rolling (Bittman and Simpson 1989). Active osmotic adjustment occurs in water-stressed wheat leaves (Morgan 1984). Measure of active osmotic adjustment is done at full turgor or by extrapolation of π vs. relative water content curve to its intercept point. We did not measure either relative water content or π at full turgor, so we cannot conclusively state that CWG has a more elastic cell wall than wheat. However, it is the most logical explanation of the very low Ψ_{md} observed for this species.

As Ψ_{md} declines, plants that can osmotically adjust to water stress show a declining π_{md} value, so the slope of the regression of π_{md} against Ψ_{md} can give an indication of osmotic adjustment (S. Angadi pers. comm.). We found a higher slope (0.61 ± 0.05 MPa MPa^{-1}) for alfalfa than for CWG (0.40 ± 0.08) or wheat (0.39 ± 0.09) ($P < 0.01$, n = 32, 28, 20 respectively, regressions not shown). This suggests that alfalfa is osmotically adjusting to water stress more than wheat or CWG.

Alfalfa exhibits high levels of abscisic acid (ABA), a plant hormone that regulates stomatal aperture and conductance of water vapour from leaf surfaces (Chen and Chen 1988). ABA control of transpirational water loss may allow alfalfa to tolerate very low Ψ_{md} observed in our study.

Alfalfa and CWG were identified as drought-tolerant forage crops during the 1930s and 1940s. Our results confirm that they respond to water stress with a different combination of strategies to avoid (alfalfa) or tolerate (CWG) leaf tissue water stress.

CONCLUSIONS

Alfalfa cultivars with very different root architecture did not differ in soil water depletion, forage yield, water use efficiency, or water potential. Both alfalfa cultivars extracted soil water to a depth of 2.7 m and this trait contributes to alfalfa's drought tolerance.

Two CWG cultivars from *Agropyron cristatum* genetic material but with contrasting ploidy (diploid vs. tetraploid) did not differ in the traits we measured.

Alfalfa and CWG used soil water during periods with no machine-harvestable aboveground growth, usually during July, August, and September. Perennial forage crops in semiarid environments maintain root and crown tissues during periods of growth dormancy and this maintenance costs soil water. The proportion of soil water used during growth dormancy can be equivalent to soil water used for forage production.

Dryland alfalfa had 30% higher WUE than CWG or wheat. These results illustrate the essential role of alfalfa for productive forage hay and pasture systems in the semiarid region of western Canada.

Alfalfa and CWG exhibited different responses to water stress. CWG exhibited very low water potentials during midday water stress, which is indicative of tissue tolerance to low water potential and very low turgor. Alfalfa exhibited apparent osmotic adjustment to maintain leaf turgor during midday water stress.

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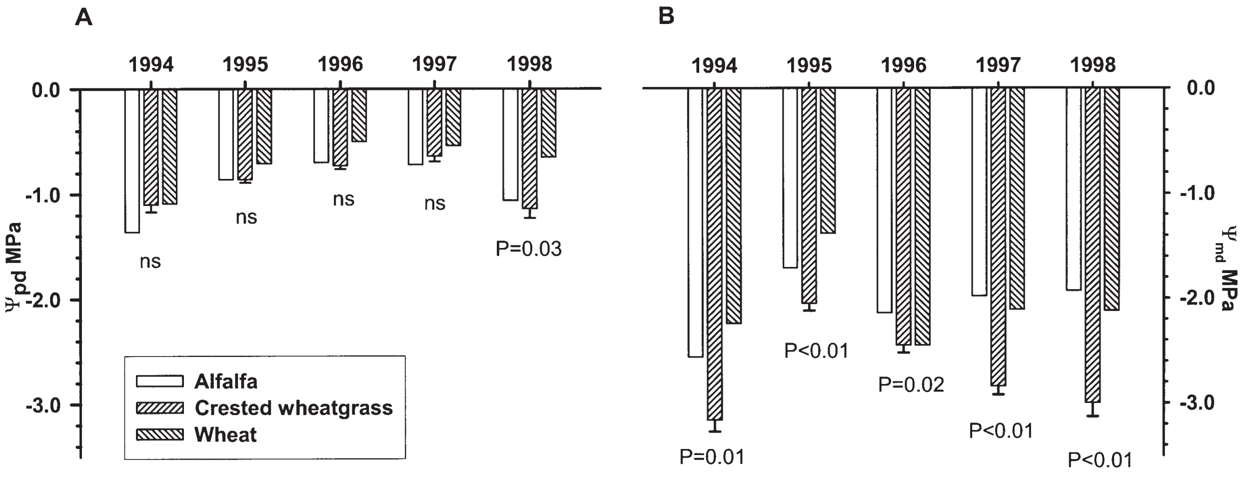

Fig. 4. Leaf water potential at predawn (Ψpd) (A) and midday (Ψmd) (B) sampling times averaged over all sampling dates within each year for 1994 to 1998 for three crop species. Vertical bars indicate SE value among means.

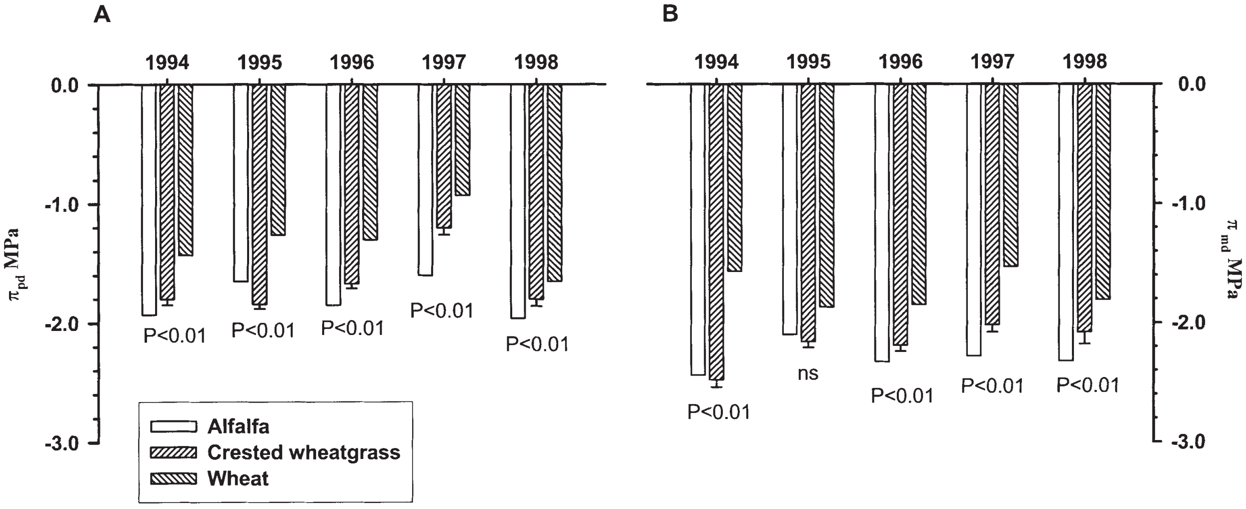

Fig. 5. Leaf osmotic potential at predawn (πpd) (A) and midday (πmd) (B) sampling times averaged over all sampling dates within each year for 1994 to 1998 for three crop species. Vertical bars indicate SE value among means.

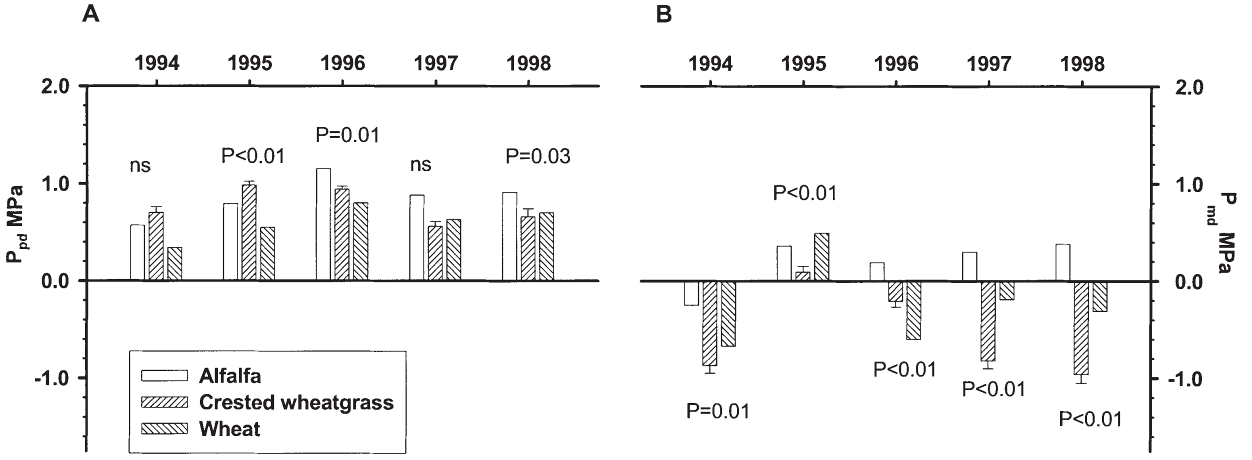

Fig. 6. Leaf turgor at predawn (P_{pd}) (A) and midday (P_{md}) (B) sampling times averaged over all sampling dates within each year for 1994 to 1998 for three crop species. Vertical bars indicate SE value among means.

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