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Environmental and Genetic Variation for Water Soluble Carbohydrate Content in Cool Season Forage Grasses

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<http://dx.doi.org/10.5772/51575>

1. Introduction

Forage dry matter has been divided into two fractions on the basis of nutritional availability. One fraction (non-structural) corresponds to the cell content and is composed of WSC (water soluble carbohydrates) (fructans and starches), lipids, most of the protein, nucleic acid and minerals. Fructan, a polymer of fructose, is accumulated as an energy reserve mainly in the leaf sheaths of temperate grasses which are made in the cytoplasm during periods of photosynthesis (Pollock and Cairns, 1991). The other dry matter fraction corresponds to the plant cell wall and consists mostly of structural carbohydrates (cellulose, hemicellulose and lignin) (Gill et al, 1989). Chemical composition of grasses changes with advancing maturity. As grass matures the proportion of the cell wall increases and the cell content fraction decreases. Together, non-structural and structural carbohydrates, depending on maturity stage, make up approximately 50 to 80% of dry matter of forages (Gill et al, 1989).

The most important traits that affecting the feeding value of herbage are digestibility (DMD), the ratios of crude protein, water-soluble carbohydrate, fiber, and the concentration of alkaloid toxins (Smith, et al., 1997; Wilkins and Humphreys, 2003). High WSC content is an important breeding goal for milk production and liveweight gain. Over a range of species, Grimes et al (1967) found strong positive correlation between WSC content and intake and liveweight gain of lambs. In the last decade, few improved ryegrass varieties had been bred for increase WSC concentration, in UK (Wilkins and Lovatt 2007; Wilkins et al. 2010), and New Zealand (Rasmussen et al., 2009). Most published data suggest that animals consuming grasses with high WSC concentrations were able to utilize the protein in their diet more efficiently, resulting in increased liveweight gain, milk production and lower loss of N (Lee et al., 2001; Evans et al., 2011; Miller et al., 2001). Similarly, Mayland et al (2001) and Smit (2006) suggested that forage with higher WSC concentration is related to

preference. In contrast, few trials that animal grazing of pure swards with high versus low concentrations of WSC, showed low (Cosgrove et al. 2010) or non significant animal performance advantages than control (Allsop et al., 2009; Parsons et al. 2010).

WSC are completely digestible and have an important role in animal nutrition, as they are a primary source of the readily available energy necessary for efficient microbial fermentation in the rumen. Fermentation of structural carbohydrates also provides energy directly to the microbial population and indirectly to the animal. Increased microbial metabolism is a prerequisite to improving forage intake and nutrient utilisation but this only occurs if the interrelationships of carbohydrate and protein are optimized (Carrier, 1994; Evans et al., 2011). One of the major problems in grasses and legumes consumption is reduced efficiency of protein utilisation and unbalanced supplies of carbohydrate and protein to support microbial metabolism (Wilkins and Humphreys, 2003). A large proportion of the protein may be lost during rumen fermentation, mainly caused by a deficiency in available carbohydrates. To increase the carbohydrate/protein ratio in the diet, either grass composition should be changed or grass should be supplemented with feeds of readily available carbohydrate. Beever and Reynolds (1994) suggested that breeding for yield and digestibility alone is no longer adequate, and that forage breeding programs should concentrate on improved nutrient value of forages, such as improved carbohydrate availability and more controlled protein degradation. Beerepoot and Agnew (1997) advised against simple selection for increased carbohydrate levels alone because of possible negative effects upon rumen pH and cell wall degradation and suggested that selection for highly digestible cell walls is preferable.

Success in conserving legumes and grasses as silage often depends on the amount of readily available fermentable carbohydrate present in herbage. If the concentration is sufficiently high, conditions are more favorable for establishment and growth of lactic acid bacteria which leads to better fermentation and preservation (Humphreys, 1994). A minimum of 3.7% WSC in fresh grass (i.e. about 15% WSC in dry weight) is considered necessary to produce good quality silage without additives (Haigh, 1990).

2. Environmental and genetic effects on WSC content

2.1. Environmental effects

WSC in forage grasses appears to be associated with good tiller survival and sward persistency (Thomas and Norris, 1981). Stored WSC provides the energy and structural carbohydrate required for growth when demand cannot be met by contemporary photosynthesis e.g. regrowth after defoliation, recovery from drought and persistency during winter (Humphreys, 1989d, 1994).

The WSC level in grasses depend on a wide range of factors, including the plant part, ploidy level, plant maturity, diurnal and seasonal effects, temperature, light intensity, growth rate, endophyte, water status, as well as the inherent differences between cultivars (Stewart and Hayes, 2011). Accumulation of WSC in tiller bases of cocksfoot is highly correlated with

summer survival and rapid recovery after drought (Volaire and Gandoïn, 1996). The amount of WSC maintained through the winter appears critical. Factors which reduce carbohydrate reserves such as autumn disease, autumn growth forced by high nitrogen application, late cutting, or uncompensated respiratory loss through growth at low light intensity, can all seriously reduce winter hardiness. If carbohydrate levels can be maintained during periods of winter growth a decline in hardiness may not occur (Humphreys, 1989d).

Radojevic et al (1994) found significant variation for WSC and DMD among four European and New Zealand varieties of perennial ryegrass under Australian conditions. A variation of 20% for WSC concentration among six diploid ryegrasses was found to be consistent over several years (Smit, 2006), the largest variation among cultivars was found during summer, in July and August. Tetraploid cultivars generally had a higher WSC concentration than diploid cultivars (Smith et al. 2001; Gilliland et al. 2002). DMD concentration declined during summer due to the influence of higher temperatures, however, high WSC lines exhibited fewer declines in DMD than the lines that did not accumulate as much WSC.

Intake depends, to some extent, on digestibility but other factors such as palatability (animal preference) are important. Jones and Roberts (1991), in a survey comparing four varieties of perennial ryegrass with the same digestibility but different WSC contents, found that varieties with high WSC content were more palatable than varieties with moderate content of WSC.

WSC content is sensitive to temperature and light intensity. Low levels of WSC are found in Western Europe country as Ireland and UK due to cloudy weather conditions (i.e. low light intensity) (Jung et al, 1996). WSC generally decline during autumn. Fulkerson and Donaghy (2001) suggested that the lower WSC concentration in autumn has several causes. The reduced solar radiation will decrease photosynthetic activity, which results in a reduced primary production of non-structural carbohydrates and WSC concentrations are closely related with hours of sunlight. The higher night temperatures in autumn will induce respiration during night time (McGrath 1988). The altering source-sink relations deplete WSC reserves, and hence lower the WSC concentration in the herbage.

There is seasonal variation in WSC content. Dent and Aldrich (1963) reported WSC content was high in spring and fell to the lowest point in summer, rising again in autumn, to about half of spring level. McGrath (1988) reported that average concentration of WSC in perennial ryegrass was 20% (mean of three cuts per year) with maximum level in late April each year. WSC content was at least 50% higher in stem than in leaf. He also reported that, on average, fructans accounted for 70% of soluble carbohydrate, the remainder being fructose, glucose and sucrose. For these reasons (environmental effects) WSC level in forage grasses vary considerably ranging from less than 5% (Waite and Boyd, 1953) to up to 50% (Bugge, 1978).

Moisture stress retards growth of grasses and is accompanied by an increase in WSC (Brown and Blaser, 1970). WSC contents can be influenced by management practices such as defoliation and nitrogen application level. Application of N fertilizer allows more rapid growth, and thus tends to result in lower levels of WSC accumulation. WSC is greatest when swards are allowed to accumulate higher herbage mass, such as silage crops, with levels

lower under very frequent grazing (Rasmussen et al. 2008). Cutting of herbage invariably causes a decrease in the amount of WSC in the remaining plant parts and this decrease reaches a minimum about one week after defoliation and is then followed by an increase associated with increasing photosynthetic activity. If cutting is repeated before the original level is restored, the successive herbage yields will be smaller and eventually such a treatment will lead to plant death. Based on this, Alberda (1966) concluded that WSC are of greater importance for the regrowth and recovery of sward after cutting. McGrath (1992) reported that application of nitrogen fertilizer increased DM yield and invariably increased CP content and decreased WSC content. However, he found no effect of nitrogen on total WSC yield.

Sowing density has a major effect on the development of individual plants. Smouter et al (1995) in a study on the effect of three tiller densities (100, 500, and 5000 plant m⁻²) on WSC concentration of *Lolium rigidum*, found that the concentration of WSC varied in response to treatment. Yield of WSC in the low-density sward was 30 to 50% higher than other swards at anthesis. In addition, the digestibility of low density was higher than of the high-density sward.

Maturity and herbage age generally have a greater influence on forage quality than environmental factors. As plants advance in maturity, cell wall concentration within stems and leaves, increases and the proportion of cell soluble content decreases. The rate of decline in digestibility of herbage is greatest during reproductive growth (Buxton et al. 1996). Breese and Thomas (1967) showed that small differences in maturity of cocksfoot could greatly affect digestibility. Rezaeifard, et al (2010) in cocksfoot grown in Iran, found that both WSC and acid detergent fiber (ADF) values increased by plant growth, however, WSC increases were slower than for ADF by advancing maturity from vegetative to milky stage. Contents of WSC were higher in stem than in leaf, so by advance of plant maturity WSC contents increase. These results are expected because with plant maturity and reducing the ratio of leaf to stem, the WSC content will increase in stem. In general, DM yield, WSC and ADF values dramatically increased by advancing of plant maturity, in contrast, DMD, CP and ash values decreased (Rezaeifard, et al., 2010). Similarly, Jafari et al (2010) in tall wheatgrass *Agropyron elongatum* and Jafari and Rezaeifard (2010) in tall fescue found the higher values of WSC-yield in pollination and milky stage under conservation management, respectively.

Humphreys (1989c) found considerable genetic variation in WSC content of ryegrass during both vegetative and reproductive growth phases. The range of variation for WSC (13.9 to 28.8%) was greater than that found for CP or DMD and WSC showed generally high heritability. Frandsen (1986) found significant variation for WSC among 36 HS families (22.9 to 44.9%) in perennial ryegrass. Wilkins and Davies (1994) also reported significant differences for WSC among four varieties of perennial ryegrass under conservation management. But, the range was relatively small (30.5 to 33.6%). Dent and Aldrich (1963), using perennial ryegrass varieties under sward condition, reported a range of 14.1 to 19.3 and 17.6 to 26.3 WSC% for frequent and conservation management, respectively.

More recently, significant variation for WSC in five phenological stages (vegetative, heading, pollination, milky and dough seed stage), were obtained in by Jafari et al (2010) in

tall wheatgrass (11.2 to 14.4%), Jafari and Rezaeifard (2010) in tall fescue (8.38 to 12.69) and by Rezaeifard, et al., (2010) in cocksfoot (7.76 to 11.37), respectively.

2.2. Gene action and heritability

By comparison to DM yield and DMD there is little information on genetic control of WSC and the extent of genetic variation in forage grasses. Estimates of three heritability estimates broad sense heritability (h^2_b), narrow sense heritability (h^2_n), and heritability, offspring/parent regression (h^2_{op}) are summarized in Table 1. Cooper (1962) reported h^2_{op} of 0.11 to 0.62 in perennial ryegrass (Table 1). Based on a diallel analysis, he estimated high $h^2_n=0.84$ and concluded that gene effects were additive (Cooper, 1973).

Contrasting results were reported by Humphreys (1989a, b). From an analysis of crosses between the early heading ryegrass, Aurora, and five late heading varieties, he found different degrees of directional dominance and over-dominance (heterosis) and concluded that WSC behaved as a complex polygenic trait, which was controlled by mainly non-additive gene effects. Genetic variation within crosses was relatively small and estimated F_2 family heritability was 0.08 to 0.14 and 0.20 to 0.38 under frequent cutting and conservation management, respectively (Table 1). In other experiments Humphreys (1995) found much higher estimates of h^2_b while the values for conservation management was again higher than that for frequent cutting (Table 1). While assessing winter hardiness of 86 accessions of perennial ryegrass under spaced plants condition, Humphreys (1989d) found significant genetic variation for WSC and estimated h^2_b from 0.38 to 0.60 for March and October harvests, respectively. In another survey he estimated h^2_b in the range of 0.27 to 0.70 for different cuts over two years in 81 accessions of perennial ryegrass (Table 1) (Humphreys, 1991).

Jafari (1998) using a polycross progeny test in ryegrass under spaced plants and swards, estimated relatively high, (h^2_b) and (h^2_n) for WSC ($h^2_b=0.60-0.80$), ($h^2_n=0.50-0.54$), respectively. The genetic analysis indicated additive genetic variances were more important for WSC and other quality traits. In another survey using full sib families of ryegrass he estimated relatively high $h^2_b=0.60$ and 0.80 for conservation and frequent cutting management, respectively (Table 1) (Jafari et al., 2003).

In other grass species some estimates of genetic control of WSC have been published (Table 1). Cooper (1962), in cocksfoot, estimated relatively high h^2_{op} which ranged from 0.78 to 0.56 for July and August cuts, respectively. Buckner et al (1981), using a polycross progeny test in *Lolium-festuca* hybrid derivatives, estimated h^2_b of 0.55 and h^2_{op} of 0.01 to 0.47 for WSC. Burner et al (1983) analyzed variance of tall fescue and obtained $h^2_b =0.55$. Grusea and Oprea (1994) found h^2_b estimates for WSC of 0.58 in cocksfoot. Jafari and Javarsineh (2005) in tall fescue and Jafari and Naseri (2007) in cocksfoot estimated relatively moderate to high values of h^2_b , while h^2_n estimates were low suggests that genetic variation in this trait is controlled by both additive and non additive gene action. Sanada, et al (2007) in cocksfoot found significant genetic variation and moderate h^2_n estimates, and suggested that forage quality of cocksfoot was influenced by an additive gene effect and could be improved genetically by recurrent and phenotypic-genotypic selection (Table 1).

Author (s)	Management/ Environment	Grass species	Basis of estimation	Heritability		
				h^2_b	h^2_n	h^2_{op}
Cooper (1962)	C/pots/ 2 cuts	<i>L.perenne</i>	FS-families			0.11 to 0.62
Cooper (1973)	C/SP/1 st cut	<i>L.perenne</i>	Diallel		0.84	
Humphreys (1989d)	C/SP/2 cuts	<i>L.perenne</i>	Populations	0.38 to 0.60		
Humphreys (1991)	C/SP/2 years	<i>L.perenne</i>	Populations	0.27 to 0.70		
Humphreys (1989b)	C/Sward/2 yr.	<i>L.perenne</i>	FS-families	0.08 to 0.38		
Humphreys (1995)	C/Sward/2 nd yr.	<i>L.perenne</i>	HS-families	0.34 to 0.71		
Jafari (1998)	C/SP/2 years	<i>L.perenne</i>	HS-families	0.75	0.50	0.26
Jafari (1998)	C/Sward/ 2 yr.	<i>L.perenne</i>	HS-families		0.54	0.17
Jafari (1998)	C/ Pots/3 yr.	<i>L.perenne</i>	HS-families	0.67	0.32	0.35
Jafari et al (2003)	C/Sward/ 2 yr.	<i>L.perenne</i>	FS-families	0.60		
Jafari et al (2003)	F/Sward/ 2 yr.	<i>L.perenne</i>	FS-families	0.80		
Jafari & Javarsineh (2005)	C/SP/ 2 yr.	<i>F.arundinacea</i>	HS-families	0.50	0.11	0.00
Burner et al (1983)	C/SP/ 2 cuts	<i>F.arundinacea</i>	Clones	0.55		
Jafari and Naseri (2007)	C/SP/2 yr.	<i>D.glomerata</i>	HS-families	0.50	0.23	0.62
Cooper (1962)	C/pots/ 2 cuts	<i>D.glomerata</i>	FS-families			0.56 to 0.78
Sanada et al (2007)	C/SP/	<i>D.glomerata</i>	HS-families	0.10	0.53	0.78
Sanada et al (2007)	C/Sward/	<i>D.glomerata</i>	Clones	0.50	0.59	
Grusea & Oprea (1994)	C/Sward/ 2 yr.	<i>D.glomerata</i>	FS-families	0.58		
Buckner et al (1981)	C/SP/ 2 nd cut	<i>Festolulium</i>	Clones	0.55		
Buckner et al (1981)	C/Sward/2 nd cut	<i>Festolulium</i>	HS-families		0.39 to 0.49	0.01 to 0.47

C, F, SP, HS, FS, Conservation management, frequent cutting management, spaced plants, Half-sib, Full-sib, respectively

Table 1. Heritability estimates for water soluble carbohydrates (WSC) in some cool-season grass species

2.3. Genotype × Environment interactions

There is little evidence for GE interaction of WSC. Burner et al (1983) reported that interaction between tall fescue genotypes and environments for WSC concentration were minor. Humphreys (1989b) reported that although WSC is a trait which is subject to large environmental fluctuations, genetic differences could remain fairly stable without large GE

interaction. He also found relative WSC contents in parents and hybrids were consistent over generations under both spaced plants and sward conditions. In contrast, Buckner et al (1981), using a polycross progeny test in *Lolium-festuca* hybrid derivatives, reported when parent and HS families were evaluated in the same environment h^2_{op} were much higher than when they were grown in different environments. They suggested that a minimum of two locations with widely different environments was necessary to develop varieties for forage quality. Conaghan et al (2008) for DM yield came to same similar conclusions. They suggested at least three locations and 2 sowing years is necessary for evaluation of perennial ryegrass trials.

Sanada, et al (2007) in cocksfoot reported a significant genotype \times year interaction for WSC and suggests that the evaluation of forage quality traits should be carried out by divergent selection under multiple environments, especially for the evaluation of parental clones. Jafari and Rezaeifard (2010) in tall fescue found non significant genotype \times phenological stage interaction effect for WSC. Similarly, Rezaeifard et al (2010) in cocksfoot reported that genotypes by environments interaction for WSC concentration were minor. This finding were in agreement of Buxton and Casler (1993), that in a review, concluded that most environment stresses have a greater effect on DM yield than on quality traits and G \times E interactions should be smaller for forage quality than for yield.

In conclusion, despite great fluctuations in WSC due to environmental and plant developmental factors, there is genetic variation within and between forage grasses populations for this character which could be exploited by selection.

3. Correlation between WSC and yield/quality traits

3.1. Correlation between WSC and Digestibility (DMD)

An understanding of the interrelationships between quality traits is important in the development of a selection program. Table 2 summarizes some of the results published for the relationships between DMD and WSC.

A broad pattern of positive phenotypic correlation between digestibility and WSC has been found for forage grasses under both conservation and frequent cutting management (Table 2). Since WSC is completely digestible a positive correlation between these two parameters is expected. The summary data for confirms that these characters show a moderate/strong positive correlation. Humphreys (1989c) found large positive correlation between DMD and WSC for spaced plants. However, under sward conditions with frequent cutting management only three of eight cuts showed significant correlation and over all cuts it was non significant (Table 2). Significant positive correlations between digestibility and WSC concentration in tall fescue forage have been reported (Burns and Smith, 1980). Bugge (1978), in Italian ryegrass, and Clements (1969), using canarygrass, found no significant correlation between DMD and WSC. Strong positive phenotypic and genotypic correlation between WSC and DMD were obtained by Jafari (1998), Jafari et al (2003) in ryegrass, Jafari and Naseri (2007) in cocksfoot, Jafari and Javarsineh (2005) in tall fescue (Table 2).

Source	Management / Nursery/ harvests	Grass species	WSC/ DMD	
			Phenotypic	Genotypic
Frandsen (1986)	C/SP/1 st Cut	<i>Lolium perenne</i>	0.76**	
Humphreys (1989c)	C/SP/annual	<i>Lolium perenne</i>	0.70**	
Dent & Aldrich (1963)	C/Sward /2 Cuts	<i>Lolium perenne</i>	0.29 to 0.51**	
Jafari (1998)	C/SP/ 2 years	<i>Lolium perenne</i>	0.89**	0.94
Jafari (1998)	C/Sward 2years	<i>Lolium perenne</i>	0.69**	0.82
Jafari (1998)	C/ Pots/3 generation	<i>Lolium perenne</i>	0.55	0.67
Jafari et al (2003)	C/Sward/ 2 years	<i>Lolium perenne</i>	0.61**	0.58
Dent & Aldrich (1963)	F/Sward	<i>Lolium perenne</i>	0.02 to 0.56**	
Grimes et al (1967)	F/Sward/annual	<i>Lolium perenne</i>	0.87**	
Humphreys (1989c)	F/Sward/ 8Cuts	<i>Lolium perenne</i>	-0.20 to 0.90**	
Jafari et al (2003)	F/Sward/ 2 years	<i>Lolium perenne</i>	0.62**	0.67
Clements (1969)	C/ Pots/3 generation	<i>Phalaris tuberosa</i>	0.16	
Buckner et al (1981)	C/SP/ 2 nd Cut	<i>Festololium</i>	0.17 to 0.57**	
Thomson & Rogers (1971)	C/Sward/2 years	<i>Phleum pratense</i>	0.12 to 0.49**	
Jafari and Naseri (2007)	C/SP/ 2 years	<i>Dactylis glomerata</i>	0.79**	0.98
Jafari and Javarsineh (2005)	C/SP/ 2 years	<i>Festuca arundinacea</i>	0.71**	0.77

*, **, Significant at 5%, 1%, respectively, respectively

SP, C, F, Spaced plant, Conservation and Frequent cutting management, respectively.

Table 2. Correlation coefficients (r) between dry matter digestibility (DMD) and water soluble carbohydrates (WSC) in some cool-season grass species.

3.2. Correlation between WSC and Crude protein (CP)

Phenotypic correlations between WSC and CP are consistent and negative across all species (Table 3). Cooper (1962) reported negative genetic correlation between WSC and CP and concluded that the limits are sufficiently wide to allow selection of a large range of protein/carbohydrate ratios. This negative relationship is present over a wide range of environment for all species. Apart from data in Table 3, there are other results which confirm this conclusion. Vose and Breese (1964), in a glasshouse study, reported high negative phenotypic relationship between WSC and CP in ryegrass. However, using covariance analysis, they suggested there is sufficient degree of genetic independence to allow simultaneous selection for both characters. Radojevic et al (1994) investigated the relationship between WSC and CP using a multiple regression analysis based on three variables (harvest date, genotype and WSC concentration). The analysis showed that the largest influences on CP concentration were time of year (72%) and genotype (5%). WSC did not explain a significant proportion of the variance of CP concentration and they concluded

that, although WSC and CP were negatively correlated, this was due mainly to divergent seasonal variation in these components of herbage. Humphreys (1989c) suggested that as growth increases with rapid uptake of nitrogen fertilizer, increase of CP and decrease of WSC content are environmentally induced effects.

Strong negative phenotypic and genotypic correlation between WSC and CP were obtained by Jafari (1998), Jafari et al (2003) in ryegrass, Jafari and Naseri (2007) in cocksfoot, Jafari and Javarsineh (2005) in tall fescue. However, Sanada et al (2007) obtained weak negative phenotypic and genotypic correlation between two traits in cocksfoot (Table 3).

Source	Management / Nursery/ harvests	Species	WSC/CP	
			Phenotypic	Genotypic
Cooper (1962)	C/Pots/2 Cuts	<i>Lolium perenne</i>		-0.20 to -0.70**
Humphreys (1989c)	C/SP/annual	<i>Lolium perenne</i>	-0.20*	
Humphreys (1989d)	C/SP/Oct. Cut	<i>Lolium perenne</i>		-0.70**
Valentine & Charles (1979)	C/Sward/3rd Cut	<i>Lolium perenne</i>	-0.61**	
Bugge (1978)	C/SP/1 st Cut	<i>Lolium perenne</i>	-0.50**	
Jafari (1998)	C/SP 2 years	<i>Lolium perenne</i>	-0.75**	-0.84
Jafari (1998)	C/Sward 2years	<i>Lolium perenne</i>	-0.69**	-0.80
Jafari et al (2003)	C/Sward/ 2 years	<i>Lolium perenne</i>	-0.65**	-0.60**
Dent & Aldrich (1963)	F/Sward	<i>Lolium perenne</i>	-0.44** to -0.69**	
Grimes et al (1967)	F/Sward/annual	<i>Lolium perenne</i>	-0.65**	
Humphreys (1989c)	F/Sward/ 8Cuts	<i>Lolium perenne</i>	-0.30 to -0.90**	
Jafari et al (2003)	F/Sward/ 2 years	<i>Lolium perenne</i>	-0.51**	-0.66**
Marais et al (1993)	F/SP/annual	<i>Lolium multiflorum</i>	-0.17 to -0.26*	-0.56**
Cooper (1962)	C/Pots/2 Cuts	<i>Dactylis glomerata</i>		-0.48* to -0.57**
Sanada et al (2007)	C/Sward/	<i>Dactylis glomerata</i>	-0.34	-0.33
Sanada et al (2007)	C/SP/	<i>Dactylis glomerata</i>	-0.14	-0.16
Jafari and Naseri (2007)	C/SP/ 2 years	<i>Dactylis glomerata</i>	-0.53*	-0.32
Clements (1969)	C/Pots/3generation	<i>Phalaris tuberosa</i>	-0.13	
Thomson & Rogers (1971)	C/Sward/2 years	<i>Phleum pratense</i>	-0.56** to -0.68**	
Jafari & Javarsineh (2005)	C/SP/ 2 years	<i>Festuca arundinacea</i>	-0.77**	-0.83

*, **, Significant at 5%, 1%, respectively, respectively

SP, C, F, Spaced plant, Conservation and Frequent cutting management, respectively.

Table 3. Correlation coefficients (r) between water soluble carbohydrates (WSC) and crude protein (CP) in some cool-season grass species.

In summary, data in Table 3 show a consistent negative correlation between WSC and CP at both phenotypic and genotypic levels and over various herbage species. It could be

concluded that, due to genetic correlation, selection for one component alone is likely to have negative effect on the other component.

3.3. Correlation between WSC and DM yield

Genotypic and phenotypic correlations between DM yield and WSC in perennial ryegrass and in other forage species are inconsistent although significant correlations are generally positive (Humphreys, 1989c). In a glasshouse study, Vose and Breese (1964) found a low and non-significant correlation between DM yield and WSC. However, Valentine and Charles (1979) obtained a highly positive correlation between DM yield and WSC particularly at low nitrogen level (Table 4).

Jafari (1998) in ryegrass found, positive and significant correlation between WSC and DM yield under spaced plant. For sward experiments their relationships were positively non significant (Jafari, 1998; Jafari et al., 2003). In contrast, Jafari and Naseri (2007) in cocksfoot, found negative and significant relationships between two traits. Jafari and Javarsineh (2005) in tall fescue and Sanada et al (2007) in cocksfoot reported low and inconsistent values between traits. The overall pattern of results suggests that DM yield and WSC are independent or show a weak positive correlation (Table4).

Source	Management / Nursery/harvests	Grass Species	WSC vs. DM yield	
			Phenotypic	Genotypic
Valentine & Charles (1979)	C/Sward/3 rd Cut	<i>Lolium perenne</i>	0.24 to 0.78**	
Humphreys (1989d)	C/SP/Oct. Cut	<i>Lolium perenne</i>		0.60**
Vose & Breese (1964)	C/Pots/4 Cuts	<i>Lolium perenne</i>		0.16
Jafari (1998)	C/SP 1 years	<i>Lolium perenne</i>	0.36*	0.61**
Jafari (1998)	C/Sward 2years	<i>Lolium perenne</i>	0.25	0.17
Jafari et al (2003)	C/Sward/ 2 years	<i>Lolium perenne</i>	0.39	0.04
Humphreys (1989c)	F/Sward/8 Cuts	<i>Lolium perenne</i>	-0.40 to 0.60**	
Jafari et al (2003)	F/Sward/ 2 years	<i>Lolium perenne</i>	0.36	0.08
Clements (1969)	C/Sward /3 years	<i>Phalaris Tuberosa</i>	0.20	
Brown & Blaser (1970)	C/Sward / 1 st Cut	<i>Dactylis glomerata</i>	0.38 to 0.82**	
Sanada et al (2007)	C/Sward/	<i>Dactylis glomerata</i>	-0.11	-0.10
Jafari & Naseri (2007)	C/SP/ 2years	<i>Dactylis glomerata</i>	-0.45**	-0.51**
Jafari & Javarsineh (2005)	C/SP/ 2years	<i>Festuca arundinacea</i>	0.04	0.06

*, **, Significant at 5%, 1%, respectively, respectively.

SP, C, F, Spaced plant, Conservation and Frequent cutting management, respectively.

Table 4. Correlation coefficients (r) between DM yield and water soluble carbohydrates (WSC) in some cool-season grass species.

4. Conclusion and grass breeding strategy

Under rotational grazing and cutting there is frequently an excess of CP in most of grasses in terms of animal requirement, particularly in autumn cuts. This excess of CP leads to high levels of rumen degradable protein (RDP). In the absence of a readily available supply of fermentable carbohydrate this can result in elevated ruminal ammonia concentrations (Beever and Siddons, 1986; Van Vuuren et al, 1986). There is also evidence that this imbalance between CP and carbohydrate has a negative influence on reproductive behavior in grazing animals (Visek, 1984; Canfield et al, 1990). Given the relationship between WSC, CP, DM yield and DMD, it is tempting to suggest that selection for high WSC is a means to improve quality in general. Beerepoot and Agnew (1997) have argued that this simple approach may not result in improved herbage quality because of possible negative effects on rumen pH. There is, however, indirect evidence that higher WSC in ryegrass may result in improved animal performance (Lee et al., 2001; Evans et al., 2011; Miller et al., 2001). Tetraploid ryegrass varieties have higher levels of WSC compared to diploids (Jung et al, 1996; Smith et al. 2001; Gilliland et al. 2002). There are two large scale animal production trials in which tetraploid and diploid varieties were compared (Castle and Watson, 1971; Connolly et al, 1977). The results from both experiments indicated that tetraploids were superior to diploids of comparable DM yield. It is possible, that this superiority was due to the slightly higher WSC content of tetraploid varieties (Smith et al. 2001; Gilliland et al. 2002). Grimes et al (1967) also found strong positive correlation between WSC content and intake and liveweight gain of lambs. On the basis of published data, it is suggested that increased WSC, particularly in the vegetative leaf and in the summer/autumn period when CP is frequently in excess, would improve herbage quality. The data also indicate that response to combined selection for both WSC and DM yield should be possible.

Abbreviations

WSC	Water soluble carbohydrates	h^2_b	Broad sense heritability
DMD	Dry matter digestibility	h^2_n	Narrow sense heritability
DM yield	Dry matter yield	h^2_{op}	Heritability, offspring/parent regression
CP	Crude protein	r_p	Phenotypic correlation
HS families	Half -sib families	r_g	Genotypic correlation

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