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Ash, Carbon Isotope Discrimination, and Silicon as Estimators of Transpiration Efficiency in Crested Wheatgrass

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Abstract

Breeding and selection for higher transpiration efficiency (*W*) has been hampered by tedious and costly methodology. Rapid and less costly methods are needed for screening *W* in plant improvement programmes. We report the relationship of ash, silicon (Si) concentration, and Si uptake to *W* in crested wheatgrass (*Agropyron desertorum* [Fischer ex Link] Schultes), an important C_3 range grass in western North America. Clones of crested wheatgrass were grown under three water levels in a field rainout shelter and as potted plants under two water levels in the field and greenhouse. Ash and Si concentrations were compared to previously determined values of shoot mass, transpiration, *W*, and carbon isotope discrimination (Δ). Ash and Si concentrations were not consistently related to Δ and *W* across all environments; however, ash concentration was positively correlated with Δ ($r=0 \cdot 69^{**}$, $df=22$) and negatively correlated with *W* ($r=-0 \cdot 61^{**}$, $df=22$) in the well-watered field environment. Across all environments and studies, the ranges in the coefficients of variation (CV, %) for clonal means were: *W*, 4–15; Δ, 1–4; ash concentration, 6–14; Si concentration, 13–30; and Si uptake, 21–33. The generally lower CV for *W*, Δ, and ash concentration suggest that these traits were more repeatable than Si concentration or uptake. Although a consistent relationship was not observed between Si and *W* and between ash and *W*, the correlations of ash and *W* from the well-watered field environment were encouraging. In view of the low cost for ash analysis, we conclude that further research is needed to evaluate the potential of ash as a criterion in selecting for improved *W*, particularly during the early phases of a breeding programme when large populations are usually involved. Later selections could be based on the more precise and accurate, but costly, Δ analysis.

Introduction

Water limits plant productivity in arid and semiarid regions of the world. To optimise plant production with limited water, plant breeders would like to select genetic material with a high productivity per unit of water transpired, i.e. high transpiration efficiency (*W*). Tedious measurements of plant growth and transpiration traditionally have been used to determine *W*. *In situ* gas exchange techniques have been used to provide estimates of instantaneous *W*; however, these measurements fail to provide an integrated value of *W* throughout the entire growing season and are not always good predictors of field *W* (Frank *et al.* 1987). Therefore, less tedious and more reliable methods are needed to estimate field *W* (Barker *et al.* 1989).

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In 1982, Farquhar and others developed theory that related *W* in C_3 plants to the level of discrimination against ^{13}C (Δ) during CO_2 fixation (Farquhar *et al.* 1989). Because C is continually being fixed by a leaf, Δ provides a long-term indication of leaf intercellular CO_2 concentration (C_i) and integrates C_i over the life of the tissue analysed. Because C_i is affected by diffusional and biochemical processes that contribute to changes in *W*, Δ may be useful in selecting plants for increased *W* (Farquhar and Richards 1984). Although Δ values calculated from measurements obtained with an isotope ratioing mass spectrometer are highly accurate and precise, they cost from $US20 to $US40 per sample. Less costly procedures for estimating *W* would be beneficial in the early phases of a plant improvement programme.

Silicon and total ash in the plant may be possible traits for economically estimating *W*. In oats (*Avena sativa* L.), Si was taken up passively (Jones and Handreck 1965) so that its accumulation in the plant was directly proportional to cumulated transpiration. However, others have found only an empirical relationship between Si uptake or Si concentration and transpiration or grain yield in wheat (*Triticum aestivum* L.) and reported that these traits were not consistently related (Paltridge and De Vries 1973; Hutton and Norrish 1974; Schultz and French 1976). Part of the difficulty in using Si uptake as an indicator of transpiration is the variability in soil-Si solubility and water uptake and the variable dust contamination on the plant material (Mayland *et al.* 1991).

Walker and Lance (1991) found that the relationship between Si content and *W* was influenced by the growth environment. They noted that barley (*Hordeum vulgare* L.) actively accumulated Si under greenhouse conditions, but passively accumulated Si under higher evaporative demand in the field. Despite this inconsistency, they concluded that Si accumulation could be used to predict *W* in field-grown barley cultivars. Masle *et al.* (1992), however, noted that whereas Si content was an unreliable predictor of *W* in several C_3 species, the sum of the mineral and to a lesser extent the ash concentrations were significantly correlated with both $1/W$ and Δ. Ranking of genotype by either trait was the same. Consequently, determination of ash and possibly Si content might provide useful and inexpensive methods for screening plants for *W*.

In this study, we report values for ash concentration, Si concentration, and Si accumulation in clones of crested wheatgrass and relate these traits to previously published data on Δ, *W*, transpiration, and shoot mass (Johnson *et al.* 1990; Read *et al.* 1991, 1992). Initially, 29 entries were grown with a soil-water gradient under a field rainout shelter. These entries were then characterised for shoot mass and Δ. Based on the Δ values, nine of these entries were selected and subsequently transplanted to pots for assessment under greenhouse conditions. Later, six of the same entries were transplanted to pots for further evaluation under field conditions.

Materials and Methods

Experiment I—Rainout Shelter

Twenty-nine clonal lines of crested wheatgrass were vegetatively propagated in a greenhouse and transplanted in May 1985 to a field site near Logan, Utah (Asay and Johnson 1990; Johnson *et al.* 1990). The experimental site, which was equipped with a rainout shelter, was on a Nibley silty clay loam (Aquic Argiustoll). A soil-water gradient was established using a line-source sprinkler system. The experimental design was a randomised-complete block with two replications and three soil water levels. On 16 June 1986, two plants of each of the 29 clones were sampled for shoot mass and leaf Δ from three areas along the gradient of water application (Johnson *et al.* 1990). Plants growing on these three areas received 30, 180, or 250 mm water during the 66 days preceding harvest. Pan evaporation during this period was approximately 300 mm.

Experiment II—Pot Studies

Nine clones of crested wheatgrass were selected from the previous study (Johnson *et al.* 1990) to represent three each of low-, medium-, and high-Δ classes for further studies in pots in both the greenhouse and field. These clones were dug from the field in either October 1989 (greenhouse phase) or March 1990 (field phase) and divided into 20–30 equal-sized ramets. The ramets were planted in plastic-lined pots (23 cm in diameter and 22 cm deep) containing 9·2 kg (greenhouse phase) or 8·2 kg (field phase) of Kidman fine sandy loam (Calcic Haploxeroll). This pot size allowed full root exploration of the soil volume and removed differences in water use attributed to differences in rooting volume. The potted soil was covered with 2 cm of perlite in the greenhouse pots and with 2 cm of pea-sized gravel in the field pots to minimise evaporation and then the pots were well watered during an adjustment phase. Well-watered and droughty treatments then were imposed (described later). Treatment combinations of clonal lines and two water levels were arranged in randomised-complete block designs in both greenhouse and field studies. Pots were weighed at 3–4-day intervals, and evapotranspiration losses were replenished by injecting water into the soil with a large syringe. Fertiliser nutrients (N, P, and K) were supplied in the water (Read *et al.* 1991, 1992). Evaporation in each environment was determined as water lost from replicated pots without plants.

Greenhouse phase

Six replications of nine clones representing three each of the low-, medium-, and high-Δ classes were subjected to a 28-day establishment period and an 84-day experimental period in a greenhouse at Logan, Utah (Read *et al.* 1991). Water levels were regularly elevated to either 120 or 30 g H_2O kg^{-1} soil, psychrometrically measured as $-0\cdot04$ and $-0\cdot1$ MPa and hereafter described as well-watered and droughty, respectively. Conditions during the October 1989 through January 1990 experimental period included: natural lighting and day length, 26/15°C average day/night temperature, and 19°C mean soil temperature.

Field phase

Read *et al.* (1992) subjected four replications of six clones representing three each of low- and high-Δ classes to a 21-day establishment period in the greenhouse and a 66-day experimental period in a field near Logan, Utah. Pots were inserted into same-sized empty pots buried in the soil. Water levels were regularly elevated to 160 or 60 g H_2O kg^{-1} soil, psychrometrically measured as $-0\cdot04$ and $-0\cdot07$ MPa and hereafter described as well-watered and droughty, respectively, in the field pots. Conditions during the April through June 1990 experimental period included: 108 mm precipitation of which approximately 8 mm fell on the pots, 345 mm pan evaporation, 23/6 °C maximum/minimum air temperature, and 13°C mean soil temperature at 10 cm depth.

Plant Tissue Preparation and Analysis

At the end of each experiment, shoots were clipped to a 5–6 cm stubble height. Plants in the rainout shelter in Experiment I were in the reproductive tiller stage with heads fully emerged (anthesis). For Experiment II, plants in the greenhouse study were in the vegetative stage, while those in the field study were at anthesis. Flag leaves and associated leaf sheaths were used for analysis in Experiment I, whereas entire shoots above 6 cm were used in Experiment II. Plant tissue was dried at 70°C for 48 h and ground to pass through a 0·35 mm (40 mesh) screen in a Wiley mill. Ash and Si concentrations were determined after dry combustion of samples in nickel crucibles at 450°C for 8 h. Ash was weighed, and then Si was determined by the colorimetric-silicomolybdous method (Fox *et al.* 1969).

Soil Si Analysis

Silicon equilibrium-solubility in soil was established by continuous shaking for 144 h in 20 mM $CaCl_2$ (40:80, soil:solution) at temperatures ranging from 5 to 43°C. The soil solutions were filtered through $<0\cdot45$ µm filter, and Si was determined as before. Silicon solubility in the Kidman soil was best described as: Si (mg/L) $= 4\cdot11 + 0\cdot42 \times$ temperature (°C), $r^2 = 0\cdot89^{**}$. Silicon solubility in the Nibley soil was calculated as: Si (mg/L) $= 12\cdot9 + 0\cdot32 \times$ temperature (°C), $r^2 = 0\cdot97^{**}$.

Statistical Methods

Data were analysed by standard regression and analysis of variance procedures. Values of Δ and shoot mass for Experiment I were obtained from Johnson *et al.* (1990), whereas *W*, Δ, shoot mass, and transpiration for greenhouse and field pot studies of Experiment II were obtained from Read *et al.* (1991) and Read *et al.* (1992), respectively. Intercharacter relationships for Experiment II were evaluated with simple correlation procedures using clonal means.

Results and Discussion

Rainout Shelter

Concentrations of ash, Si and previously determined values of Δ increased linearly ($P<0{\cdot}05$) with water application in the field rainout shelter (Table 1). Differences between clonal means for shoot mass and Si and ash concentration were consistent across water levels as indicated by the non-significant water × entry interaction. Values for Si and ash concentration were positively correlated ($P<0{\cdot}01$) with each other and with Δ (data not shown). Because W is inversely related to Δ in crested wheatgrass (Johnson *et al.* 1990; Read *et al.* 1991, 1992), selecting for lower values of ash and Si concentration would lead to increased W.

Table 1. Means of shoot mass, carbon isotope discrimination (Δ), and Si and ash concentration on a dry weight basis in flag leaves and sheaths of 29 crested wheatgrass entries grown in a field rainout shelter at three water levels

Water was applied during the period from 11 April to 18 June 1986. Linear effect of water level on each trait was significant ($P\leqslant 0{\cdot}05$). Data for shoot mass and Δ are from Johnson *et al.* (1990)

Water level (mm)	Shoot mass (g plant^{-1})	Δ (‰)	Si concn (mg g^{-1})	Ash concn (mg g^{-1})
30	150	18·4	18·3	102
180	215	19·8	26·7	129
250	254	20·3	34·8	141

Pot Studies

Correlations among W, Δ, Si uptake, Si and ash concentration, shoot mass, and transpiration were calculated for both greenhouse and field pot studies within the well-watered and droughty treatments (Table 2). Silicon concentration and uptake were negatively related to W only in the well-watered treatment in the greenhouse. Ash concentration was not significantly related to W in either the well-watered or droughty treatments in the greenhouse, but was negatively related ($P<0{\cdot}01$) to W ($r=-0{\cdot}61$, 22 df) in the well-watered treatment in the field pot study (Fig. 1). These results from the field suggest that ash concentration may hold promise for estimating W in crested wheatgrass grown under favourable water conditions.

The larger vapour pressure deficits that occurred in the field compared to the greenhouse increased transpiration and the uptake of Si (Table 3), particularly in the well-watered treatment where more water was available. Traits in the well-watered plant tissue generally were measured with more precision than plant tissue exposed to drought. This smaller error in measurement might explain the higher correlations between ash concentration, W, and Δ in the well-watered compared to droughty plants. The high correlation between ash content and W found by Masle *et al.* (1992) for various C_3 species also was obtained for plants grown under ample supply of water and nutrients. We did not wash the harvested plant material to remove exogenous dust from the leaves. If such contamination was a factor, washing the samples prior to analysis might improve the relationship between ash or Si uptake with transpiration, Δ, and W.

Ash and Si concentration were determined with less precision than Δ (Table 3). In these differing soil-water environments, CV values ranged from 1–4% for Δ, compared to CV values of 13–30% for Si concentration, 21–33% for Si uptake, and 6–14% for ash con-

Table 2. Correlation (*r*) matrix of transpiration efficiency (*W*), carbon isotope discrimination (Δ), and other traits for crested wheatgrass plants grown with well-watered (upper right) or droughty (lower left) treatments in pots in the greenhouse (9 clonal lines) and field (6 clonal lines)

*, ** indicate significant differences at the 0·05 and 0·01 probability levels, respectively (*df* are 52 for greenhouse and 22 for field). Data on the diagonal represent the correlations of well-watered versus droughty treatments for given parameter. Example: In greenhouse pots, Δ and *W* of well-watered (ww) plants have $r = -0·83$, Δ and *W* of droughty (D) plants have $r = -0·78$, and Δ of ww and Δ of D have $r = 0·16$. Data for *W*, Δ, shoot mass, and transpiration were obtained from Read *et al.* (1991, 1992)

Droughty	Well-watered						
	W	Δ	Si concn	Si uptake	Ash concn	Shoot mass	Transpiration
			Greenhouse pots				
W	**0·26**	−0·83**	−0·41**	−0·57**	0·07	−0·61**	−0·82**
Δ	−0·78**	**0·16**	0·32*	0·53**	−0·27*	0·65**	0·77**
Si concn	0·19	−0·02	**0·30**	0·84**	0·34*	0·37**	0·38**
Si uptake	0·18	0·05	0·83**	**0·38**	0·11	0·80**	0·77**
Ash concn	0·18	−0·09	0·74**	0·55**	**0·33**	−0·22	−0·17
Shoot mass	0·11	0·10	−0·19	0·36**	−0·32*	**0·39**	0·94*
Transpiration	−0·63**	0·67**	−0·18	0·24	−0·27*	0·68**	**0·33***
			Field pots				
W	**0·71**	−0·86**	−0·29	−0·08	−0·61**	0·46*	−0·33
Δ	−0·75**	**0·73**	0·25	0·02	0·69**	−0·52**	0·15
Si concn	0·25	−0·08	**0·52**	0·92**	0·68**	−0·07	0·15
Si uptake	0·06	−0·04	0·95**	**0·54**	0·42*	0·31	0·38*
Ash concn	0·10	0·12	0·64**	0·54**	**0·57**	−0·55	−0·09
Shoot mass	−0·62**	0·16	−0·26	0·06	−0·31	**0·20**	0·68**
Transpiration	−0·91**	0·62**	−0·29	−0·02	−0·15	0·84**	**0·22***

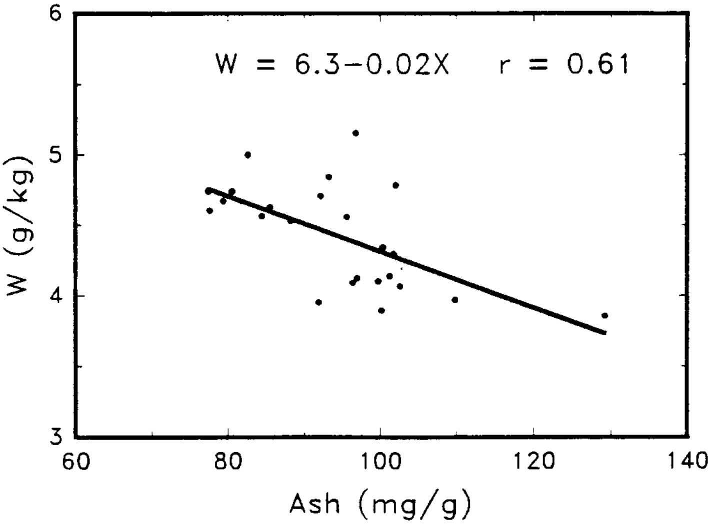

Fig. 1. Relationship between transpiration efficiency (*W*) and ash concentration in crested wheatgrass plants growing in well-watered pots under field conditions.

Table 3. Summary statistics of various traits measured for crested wheatgrass grown in five environments. Data are for flag leaves and sheaths, except for shoot biomass which included flowering heads Data for W, Δ, shoot mass, and transpiration were obtained from Read *et al.* (1991, 1992). $A:C$, ratio of actual Si uptake to calculated Si uptake

	W (g kg^{-1})	Δ (‰)	Si concn (mg g^{-1})	Si uptake (mg)	Si $A:C$	Ash concn (mg g^{-1})	Shoot mass (g)	Transpiration (kg plant^{-1})
Field pots, well-watered								
Minimum	4·0	18·8	4·1	318	2·0	86	68	16·7
Maximum	4·9	20·4	5·5	482	2·6	110	88	19·7
Mean	4·4	19·5	4·9	374	2·2	94	77	18·1
SE	0·2	0·3	1·5	123	0·2	9	6	1·6
CV (%)	4	1	30	33	31	10	8	9
Field pots, droughty								
Minimum	7·6	15·6	3·6	168	2·7	94	43	4·6
Maximum	10·8	17·8	5·0	229	4·5	106	49	7·0
Mean	9·3	16·5	4·3	192	3·8	100	45	5·6
SE	1·2	0·4	1·2	52	1·4	8	4	1·2
CV (%)	13	3	29	27	37	8	10	22
Greenhouse pots, well-watered								
Minimum	1·5	23·0	6·0	47	1·2	108	8	3·7
Maximum	2·2	24·3	10·8	106	1·8	129	13	8·1
Mean	1·7	23·9	7·9	78	1·4	120	10	5·8
SE	0·2	0·4	1·0	16	0·2	7	1	1·0
CV (%)	10	2	13	21	15	6	14	16
Greenhouse pots, droughty								
Minimum	1·7	21·1	3·8	26	0·8	103	5	2·3
Maximum	2·5	23·2	7·6	49	1·7	123	7	4·0
Mean	2·1	22·2	6·0	38	1·3	114	6	3·2
SE	0·4	0·6	1·5	12	0·5	6	1	0·6
CV (%)	15	3	25	31	40	6	15	18
Rainout shelter, combined water levels								
Minimum	–	18·0	16·2	–	–	89	136	–
Maximum	–	21·2	35·3	–	–	150	268	–
Mean	–	19·5	27·0	–	–	125	206	–
SE	–	0·8	5·1	–	–	17	44	–
CV (%)	–	4	19	–	–	14	21	–

centration. The CV values for transpiration ranged from 9–22%, and those for W ranged from 4–15%. Plant ash concentration was measured with similar precision in both water treatments, whereas the other traits were measured with greater precision in well-watered than droughty treatments. The generally lower CV values for W, Δ, and ash concentration suggest that these traits are more repeatable than those of Si uptake or Si concentration.

No differences were found between the Δ classes for Si concentration or uptake in the field (Table 4); however, in both the well-watered and droughty treatments in the greenhouse, Si concentration for the low-Δ class was significantly higher than for the high-Δ class. The results for Si uptake are disappointing because others have shown an empirical relationship between Si uptake and W in barley, oats, and wheat (Jones and Handreck 1965;

Table 4. Transpiration efficiency (W), carbon isotope discrimination (Δ), and other traits of low-, medium-, and high-Δ classes of crested wheatgrass clones grown in five environments. There were three entries per group with 4 replications in the rainout shelter, 6 replications in the greenhouse study, and 4 replications in the field study

Within traits and environments, class means followed by different letters are significantly ($P<0{\cdot}05$) different according to Duncan's means separation test. Values for W, Δ, shoot mass, and transpiration are from Johnson *et al.* (1990) and Read *et al.* (1991, 1992). Grouping is based on Δ values for clones grown in rainout shelter (Johnson *et al.* 1990). W, transpiration, Si uptake, and Si ratio $A:C$ were not determined for rainout-shelter environment. Si and ash concentration are for flag leaf and associated sheath, not entire shoot for rainout shelter environment

Group	Rainout shelter	Greenhouse		Field	
		Well-watered	Droughty	Well-watered	Droughty
		W (g kg^{-1})			
Low		1·7b	2·2a	4·6a	10·3a
Medium		1·9a	2·2a		
High		1·7b	1·9b	4·3b	8·2b
		Δ (‰)			
Low	18·3c	24·1a	21·7c	19·1b	15·7b
Medium	19·6b	23·8b	22·1b		
High	20·2a	24·0ab	22·7a	19·8a	17·2a
		Si concn (mg g^{-1})			
Low	26·1b	7·5b	5·4b	4·7a	4·2a
Medium	27·7a	7·5b	5·9ab		
High	24·6b	8·7a	6·7a	5·0a	4·3a
		Si uptake (mg plant^{-1})			
Low		84a	37a	390a	190a
Medium		68b	35a		
High		80a	40a	360a	200a
		Ash (mg g^{-1})			
Low	125a	120a	110b	91b	99a
Medium	131a	120a	120a		
High	128a	120a	120a	98a	99a
		Shoot mass (g plant^{-1})			
Low	190a	11a	7a	82a	45a
Medium	210a	9b	6b		
High	210a	9b	6b	73b	46a
		Transpiration (kg plant^{-1})			
Low		6·8a	3·2ab	18·5a	4·9b
Medium		5·1b	2·9b		
High		5·4b	3·3a	17·7a	6·2a
		Si ratio (actual:calculated flow)			
Low		1·3b	1·2a	2·2a	4·1a
Medium		1·4a	1·4a		
High		1·5a	1·3a	2·2a	3·5a

Hutton and Norrish 1974; Mayland *et al.* 1991; Walker and Lance 1991). Ash concentrations were significantly ($P<0\cdot05$) greater in the high than in the low Δ classes in the droughty treatment in the greenhouse and in the well-watered treatment in the field, but this relationship was not consistent across all environments.

Shoot mass (Table 4) was not different among Δ classes for plants grown in the rainout shelter or the droughty field treatment. However, yield was greater ($P<0\cdot05$) by 10–20% for plants in the low- compared to the high-Δ class for both water treatments in the greenhouse and for the well-watered field environment. This suggests that additional research is needed to clarify the relationship between Δ and forage yield.

Silicon Uptake

Silicon uptake may be a useful indicator of transpiration when the flux ratio (mg Si kg^{-1} H_2O) in the transpiration stream is the same as in the soil solution. This is the flux ratio of actual Si uptake to that calculated from mass flow and is identified as $A:C$. The mean flux ratio for the field pot study ranged from 2·2 to 3·8, being higher for the droughty treatment. The ratio in the greenhouse pot study averaged 1·4 in the well-watered and 1·3 in the droughty treatment (Table 3). Van der Vorm (1980) noted that Si uptake was different for the five species tested in solution culture and that the ratio was dependent upon solution Si concentration. Mayland *et al.* (1991) found that flux values increased with drought.

Silicon uptake may be useful as an indicator of transpiration if Si is taken up passively with the transpiration stream and accumulated in plant tissue. If this were the case, then the Si concentration also would be the same in the transpiration stream as in the soil solution and the flux ratio would be equal to 1·0. Flux ratios less than 1·0 indicate that plants are able to prevent the absorption and/or translocation of Si to the shoots, and many non-grasses exhibit this pattern. Plants that actively absorb Si, typically have flux ratios greater than 1·0, except when the rooting solution contains very high concentrations of soluble Si. Many grasses, with the possible exception of oats, have ratios greater than 1·0 under field conditions where the soil-Si equilibrium concentrations range between 2·8 mg L^{-1} for quartz and 51 mg Si L^{-1} for amorphous silica (Jones and Handreck 1965; Handreck and Jones 1968; Elgawhary and Lindsay 1972; Paltridge and De Vries 1973; Van der Vorm 1980; Jarvis 1987; Mayland *et al.* 1991). Crested wheatgrass, similar to barley, ryegrass, and wheat, apparently exhibits some active uptake of soil-solution Si (Van der Vorm 1980; Jarvis 1987; Mayland *et al.* 1991). For field pot environments, the flux ratio ($A:C$) was closer to 1·0 for plants grown in well-watered than for those in droughty soil (Table 3). Therefore, ash and Si probably would best predict W when determined in well-watered plants.

In summary, a close relationship was observed in crested wheatgrass between ash concentration and W for the well-watered treatment in the field pot study. This relationship should be evaluated further with larger field populations in several environments. If such a relationship can be substantiated, large populations could be screened relatively cheaply for ash content in the early phases of a breeding programme, as suggested by Masle *et al.* (1992). Clones selected from this initial screening could then be analysed for Δ by the more precise and accurate, but more costly, mass spectrometer analysis.

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