Response of eight Canadian spring wheat (*Triticum aestivum* L.) cultivars to copper: Pollen viability, grain yield plant^{-1} and yield components

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Owuoche, J. O., Briggs, K. G., Taylor, G. J. and Penney, D. C. 1994. **Response of eight Canadian spring wheat (*Triticum aestivum* L.) cultivars to copper: Pollen viability, grain yield plant^{-1} and yield components.** Can. J. Plant Sci. **74**: 25–30. Eight Canadian spring wheat (*Triticum aestivum* L.) cultivars, Katepwa, Roblin, Park, Laura, Conway, Oslo, Columbus and Biggar, were tested in the field for copper (Cu) use efficiency. The experiment was conducted at Stony Plain, Alberta on an Orthic, Dark Grey, Chernozemic, Cu deficient (0.48 $\mu g\ g^{-1}$) soil. A split-plot experimental design was used with (+Cu) and without (−Cu) copper treatment of 12.2 kg copper sulphate ha^{-1}. Significant ($P \leq 0.05$) effects due to cultivar, Cu, season, and cultivar × Cu interaction were observed, indicating differential response of the test cultivars to Cu for yield and yield components. Cu application significantly ($P \leq 0.05$) improved the number of grains spike^{-1}, and floret fertility of Roblin, Laura, Park and Oslo, and increased the grain yield of Conway by 10%. Significant ($P \leq 0.05$) effects due to cultivar, year and year × cultivar interaction for Cu efficiency indicated that Cu use efficiency varied with both year and cultivar. Biggar showed the highest Cu use efficiency (108%) while Oslo showed the lowest (57%).

Key words: *Triticum aestivum* L., cultivars, copper, pollen viability, copper use efficiency

Owuoche, J. O., Briggs, K. G., Taylor, G. J. et Penney, D. C. 1994. **Réaction au cuivre de huit cultivars canadiens de blé de printemps (*Triticum aestivum* L.): viabilité du pollen, rendement en grain par plante et composition du rendement.** Can. J. Plant Sci. **74**: 25–30. Huit cultivars canadiens de blé de printemps (*Triticum aestivum*): Katepwa, Roblin, Park, Laura, Conway, Oslo, Columbus et Biggar ont été évalués au champs pour leur efficacité d'utilisation du cuivre (Cu). L'expérience était réalisée à Stony Plain, Alberta sur un sol tchernozémique gris foncé orthique carencé en Cu (0,48 g g^{-1}). Un dispositif expérimental en parcelles divisées a été utilisé: sans Cu et avec apport de Cu (12,2 kg sulphate de cuivre par hectare). Les effets significatifs ($P \leq 0{,}05$) dus aux cultivars, au traitement de Cu, à la saison et à l'interaction cultivar × Cu étaient observés, révélant une réaction différentielle des cultivars au Cu pour le rendement et pour les composantes du rendement. L'apport de Cu apportait une amélioration une significative ($P \leq 0{,}05$) du nombre de grains par épi ainsi que de la fertilité des florules chez Roblin, Laura, Park et Oslo. En outre, il accroissait de 10% le rendement grainier de Conway. Les effets significatifs ($P \leq 0{,}05$) sur l'efficacité de l'utilisation de Cu, dus aux cultivars, à l'année et à l'interaction année × cultivar donnent à penser que cette efficacité varie à la fois selon l'année et selon le cultivar. Biggar démontrait la plus grande efficacité d'utilisation (108%) et Oslo la moins bonne (57%).

Mots clés: *Triticum aestivum* L., cultivars, cuivre, viabilité du pollen, efficacité d'utilisation du cuivre

Copper (Cu) deficiency affects the growth and development of wheat (*Triticum aestivum*) in many ways. During the reproductive phase, Cu deficiency causes pollen sterility, a reduction in pollen number, and dented, small, and starchless pollen in wheat and barley (*Hordeum vulgare*) (Graham 1975; Jewell et al. 1988). These findings led to the hypothesis that insufficient carbohydrates in pollen grains cause infertility. Graham (1976) suggested that Cu deficiency interferes with microsporogenesis during the process of meiosis at the early booting stage in wheat plants.

Copper sulfate and copper oxide have been used to correct Cu deficiency in commercial wheat production in Australia (Graham et al. 1981; Alloway and Alison 1984). In Kenya, copper oxychloride has been applied as a seed dressing and foliar feed in commercial wheat farms for over two-and-half decades (Pinkerton 1967). Application of copper oxychloride provides multiple effects on the plant by increasing vigour, grain yield, and protection from fungal infections (Graham 1984).

Various Cu compounds demonstrate efficacy as soil and foliar fertilizers on wheat and barley. For example, copper oxide is ineffective in the year of application, but alleviates deficiencies in the subsequent year, while copper sulphate (bluestone) and chelated products are effective in the year of application (Karamanos et al. 1986). Low soil moisture enhanced Cu deficiency in subterranean clover (*Trifolium subterranean* L. 'Seaton Park') (Reuter et al. 1981) and in wheat (Grundon 1991). Moisture levels might therefore be expected to influence the availability of Cu for uptake.

The objective of this field study was to determine the response of eight Canadian spring wheat cultivars to Cu application, on an Orthic, Dark Grey, Chernozemic, Cu-deficient soil at Stony Plain, Central Alberta, by evaluating pollen viability, grain yield and components of grain yield of individually sampled plants.

MATERIALS AND METHODS

Site

A field experiment was conducted for two seasons (1990 and 1991) at Stony Plain, Central Alberta (53°02′N - 114°00′W), about 50 km west of Edmonton. The soil at the experimental site was an Orthic, Dark Grey Chernozem, which originated from deltaic material (Alberta Soil Survey 1970) and was previously characterized to be Cu deficient. The field on which the experiment was conducted had previously produced a barley crop. Prior to the experiment, soil samples from a 0–15 cm furrow slice were collected, bulked and analyzed (Table 1).

Treatments

Eight Canadian spring wheat cultivars (Katepwa, Roblin, Park, Laura, Conway, Oslo, Columbus, and Biggar) were selected on the basis of differing agronomic characteristics. Katepwa and Columbus are respectively medium and late in maturity, while Roblin and Park are early. All are awnless, and Park has been reported to be sensitive to Cu deficiency (Piening et al. 1985). Oslo is semi-dwarf, awned, medium in maturity and well adapted to Central Alberta. Biggar is semi-dwarf, awned and very late in maturity. Conway and Laura are medium in maturity.

In 1990, the land was prepared using a disc plough until a fine tilth suitable for seeding wheat was achieved. A split-plot experimental design with four replicates was used with cultivars planted in the same plots for the two growing seasons. Cultivars were the main-plot factor, and copper treatment was the sub-plot factor. The 1990 experimental area was accurately marked for subsequent placement of the 1991 trial. In 1991 each plot was tilled and rotovated separately to avoid mixing of the soil from +Cu plots with that in the −Cu plots from the previous season treatments. Trials were seeded with a disc drill set at 17.5-cm row spacing. Plots were 13.7 m long by 1.4 m wide. The seeding rate was 84 kg seed ha^{-1}, using seed of 95% or better germinability which had been dressed with Vitavax to control seed borne and soil borne diseases. The sub-plots were separated by 0.5-m wide non-planted alleys and 4.8 m was left between blocks. Nitrogen, phosphorus, potassium and sulfur were worked into the soil at the rate of 67 kg ha^{-1} (N), 50 kg ha^{-1} (P), 34 kg ha^{-1} (K) and 11 kg ha^{-1} (S) using a rotovator. Copper sulphate fertilizer was supplied with the seed at the rate of 12.2 kg ha^{-1} in 1990 and as chelate in 1991 on the +Cu treatment, while in the control no copper was applied (−Cu). Weeds were controlled by pre-emergence herbicide (triallate) at the rate of 1.5 kg ha^{-1} and post-emergence herbicide (diclofop-methyl) at the rate of 0.78 kg ha^{-1}, applied 28 d after sowing. The non-planted alleys were mechanically weeded using a rotovator. The distribution of rainfall and the mean maximum and minimum temperatures for each growing month were recorded (Table 2). Total growing season precipitation was 349 mm in 1990 and 306 mm in 1991.

Table 1. Characteristics of the Orthic, Dark Grey, Chernozemic soil sampled from the experimental site (Stony Plain) in 1990

Characteristic	
Soil pH($CaCl_2$)	5.41
Cu	0.48^z
B	0.45^z
Mn	71.21^z
Zn	14.05^z
Fe	164.60^z
Organic matter, %	8.90

^{z}Micronutrient in μg g^{-1} soil, analyzed using Diethylene triamine penta-acetic acid.

Table 2. Mean rainfall and temperatures experienced during 1990 and 1991 at Stony Plain

		May	June	July	August
1990					
Rainfall (mm)		50.6	52.7	159.6	85.6
Mean temp (°C)	Max.	16.6	19.7	21.6	21.7
	Min.	4.9	9.5	11.5	11.3
1991					
Rainfall (mm)		98.7	105.5	24.0	78.0
Mean temp. (°C)	Max.	16.7	18.5	22.7	24.4
	Min.	5.3	9.6	11.5	12.6

Pollen Viability

Pollen grains were stained with iodine-potassium iodate to identify cultivars producing sterile pollen grains. Five spikes with 50% anthers extruded at anthesis were sampled at random from each sub-plot from all replicates. Spikes were labelled and placed in conical flasks filled with water to avoid wilting during transportation from the experimental site. The glumes and paleas were clipped from each spike, which was then left for a few minutes to allow the anthers to extrude and dehisce. Each spike was then gently tapped over a slide so the dehisced anthers could shed the pollen grains. These pollen grains were immediately stained with 80% ethyl alcohol and iodine-potassium iodate solution for 90 s and covered with plastic slips, using the method of Graham and Pearce (1979). A random sample of 250 pollen grains per spike was evaluated under a light microscope (× 400), and non-stained grains were counted. Only pollen grains that were fully stained were considered viable. Percent pollen stain was then calculated.

Grain Yield Plant^{-1}, Yield Components and Percent Fertile Florets Spike^{-1}

Most plots were harvested at the beginning of September in 1990, but in 1991 harvesting was completed by the end of August. For spike length measurements, 10 plants were sampled at random from the inner six rows of the second half of each sub-plot. After determining the number of tillers plant^{-1}, the spikes from the main stems and tillers were separated for the determination of the number of florets

Table 3. Mean squares for grain yield plant^{-1}, yield components, percent pollen stain and percent fertile florets spike^{-1}, of eight Canadian spring wheat cultivars (*T. aestivum* L.)

			% fertile florets spike^{-1}		Number of grains spike^{-1}		1000-kernel weight (g)			
Source	df	% pollen stain	Main stem	Tillers	Main stem	Tillers	Main stem	Tillers	Grain yield plant^{-1} (g)	% Cu use efficiency for grain yield plant^{-1}
Replicate	3	95.1	210.6	289.6	50.6	171.8	9.7	1.5	0.4	188
Cultivar	7	184.3**	358.9**	510.0**	902.0**	509.5**	45.6**	71.8**	25.3**	486*
Cultivar × Rep (E_a)	21	22.8	37.8	41.2	35.5	25.3	10.4	9.3	0.6	—
CV%		7.1	11.2	12.5	15.2	23.8	9.3	9.3	18.3	—
Cu	1	735.8**	669.2**	1393.2**	697.8**	819.1**	44.3**	1.4	19.4**	—
Rep × Cu	3	11.3	50.7	34.6	33.8	35.5	26.0	15.6	0.2	—
Cultivar × Cu	7	43.4	45.0	61.8	46.1	43.4	9.9*	6.0	1.9	—
Rep × Cu × Cultivar (E_b)	21	28.1	37.8	31.6	35.1	31.0	3.5	6.2	1.5	—
CV%		7.8	11.2	11.0	17.8	22.3	5.3	7.7	27.3	—
Year	1	1337.3**	474.5**	1017.3**	83.8	424.1**	236.3**	75.8**	9.7**	3282**
Year × Cultivar	7	46.4	87.2**	92.3*	40.1	29.9	45.5**	48.0	3.3*	470*
Year × Cu	1	84.7	207.0**	187.7*	301.5**	76.0	22.2	24.2	19.1**	—
Year × Cultivar × Cu	7	15.8	67.4*	50.5	61.7*	28.5	8.3	8.0	1.4	—
Error	48^z	27.8	27.3	38.2	24.1	23.0	8.6	8.5	1.2	172
CV%		7.8	9.6	12.1	14.8	19.2	8.4	8.9	24.6	20.4

^{z}43 df for percent copper efficiency use for grain yield plant^{-1}.
*,**Significant at $P \leq 0.05$ and at $P \leq 0.01$ respectively; CV% = coefficient of variation, percent.

Table 4. Effects of copper on pollen viability and floret fertility of eight Canadian spring wheat cultivars

			% fertile florets spike^{-1}			
	% pollen stain		Main stems		Tillers	
Cultivar	−Cu	+Cu	−Cu	+Cu	−Cu	+Cu
Katepwa	84.4	92.3**	71.0	76.4	67.0	75.3
Roblin	71.6	85.6**	60.0	67.4*	51.1	62.3*
Park	72.9	80.9*	58.2	65.5	46.6	61.2
Laura	77.8	83.5	53.6	70.1*	43.9	60.9*
Conway	83.5	89.0**	63.4	71.5*	58.1	70.0*
Oslo	81.2	88.2*	50.7	65.4*	38.6	57.5*
Columbus	84.5	86.6*	59.3	60.9	59.2	60.8
Biggar	87.4	88.0	78.0	80.1	73.1	74.8
Mean Cu effect		+6.2**		+7.9**		+10.8**

*,**Significant at $P \leq 0.05$ and $P \leq 0.01$ respectively.

spike^{-1}, grains spike^{-1}, 1000-kernel weight, and grain yield plant^{-1}; 1000-kernel grain weight was determined by weighing a sample of 100 grains from spikes of the main stems and tillers, selected separately at random. Percent fertile florets spike^{-1} was computed as the ratio of the number of grains spike^{-1} to the number of florets spike^{-1}. The percent Cu use efficiency was calculated by expressing grain yield plant^{-1} from the −Cu treatment as a percent of that from the +Cu treatment of each replicate.

Statistical Analyses

Combined year split-plot analyses were used to assess the differences among cultivars, treatments, and the cultivar × Cu interaction, for grain yield plant^{-1} and yield components. The data for percent stained pollen, fertile florets and percent Cu use efficiency for each replicate were transformed using arc sine in order to obtain homogeneous variances. The Student *t*-test was used for comparing significant differences between +Cu and −Cu treatment means of each cultivar for grain yield and for yield components.

RESULTS

Effects of Copper on Pollen Viability

Light microscope observations indicated that the size of pollen grains varied between cultivars, and grains from Cu-deficient treatments showed dented conformation. Pollen grains could be separated into one of three categories, (1) fully stained, (2) partially stained, and (3) non-stained and dented. Only fully stained grains were considered viable.

Cu fertilization resulted in a significant ($P \leq 0.05$) percent increase of 6.2% in pollen viability and 7.9 and 10.8% in floret fertility of main stems and tillers, averaged over all cultivars (Tables 3 and 4). All cultivars responded for pollen viability except Laura and Biggar. In the −Cu treatment, Biggar had the highest mean pollen viability while Roblin had the lowest. The highest mean percent viable pollen was observed from Katepwa in the +Cu treatment. Cu treatment significantly ($P \leq 0.05$) improved the floret fertility of Roblin, Laura, Conway and Oslo with the largest responses observed on Laura and Oslo. No significant responses to Cu level by percent fertile florets spike^{-1} were observed for the remaining cultivars.

Effects on Grain Yield Plant^{-1}, Yield Components and Percent Fertile Florets

Cultivar effects were significant ($P \leq 0.01$) for all variables (Table 3). Significant ($P \leq 0.05$) effects due to Cu were observed on all variables, except for 1000-kernel weight on tillers. Year effects were significant ($P \le 0.01$) for all variables except number of grains spike^{-1} on the main stem. Significant ($P \le 0.05$) year × cultivar interactions occurred for the number of fertile florets spike^{-1} (mainstem and tillers) and for 1000-kernel weight on the mainstem. The year × Cu interaction was significant ($P \le 0.05$) for the number of fertile florets spike^{-1} on the main stem and tillers, and for grain yield plant^{-1}.

Significant ($P \le 0.01$) main effects were found due to Cu for grain yield plant^{-1} and most yield components (Tables 3 and 4). A significant ($P \le 0.05$) cultivar × Cu interaction was only observed for 1000-kernel weight from main stems (Table 3). The response of individual cultivars, averaged over two years, is indicated in Table 5. Significant ($P \le 0.05$) increases in 1000-kernel weight from main stems, due to Cu application, were observed for Katepwa, Laura, Conway, and Oslo. Columbus demonstrated high mean 1000-kernel weight on both −Cu and +Cu treatments but its grain yield or components did not respond significantly to treatment with copper. No significant increase in 1000-kernel weight due to Cu application was observed on grains from the tillers, for any cultivar.

Significant (≤ 0.05) response to Cu for number of grains spike^{-1} was observed on the main stems and tillers of Roblin, Park and Oslo (Table 5). Conway showed significant ($P \le 0.05$) response to Cu for the number of grains spike^{-1}, but only on the tillers. Biggar had the largest number of grains both on the main stems and tillers, but showed no significant response to Cu fertilization for this trait.

As previously indicated, significant ($P \le 0.05$) effects due to cultivar and Cu treatment were observed for grain yield plant^{-1}. Roblin and Oslo both showed significantly increased grain yield plant^{-1} after Cu fertilization, and Oslo also demonstrated the lowest Cu use efficiency. Biggar showed the highest grain yield plant^{-1} in both Cu treatments, but did not respond to copper fertilization. Cu use efficiency values ranged from a high of 108.4% (Biggar) to a low of 57.6% (Oslo). Cu use efficiency of Conway was not significantly different from that of Biggar, but its grain yield plant^{-1} was significantly lower (Table 5).

Effects of Year

Year effects were significant ($P \le 0.01$) for all variables except number of grains per spike on the main stem (Table 3). Significant ($P \le 0.05$) year × cultivar interaction for percent floret fertility, 1000-kernel weight on the mainstem, grain yield plant^{-1} and Cu use efficiency, all indicated differential performance of the test cultivars in different seasons. Significant ($P \le 0.05$) year × Cu interaction for percent floret fertility (mainstem and tillers), number of grains spike^{-1} (mainstem), and grain yield plant^{-1} suggest that the effects of applied soil Cu on the cultivars were subject to moisture regime, which differed markedly in the 2 yr (Table 2). For % floret fertility and the number of grains spike^{-1} of the main stem, a significant ($P \le 0.05$) interaction for the year × cultivar × Cu effects was also observed. This interaction also illustrated that the test cultivars responded differently to Cu supply in different growing seasons. This was also found for percent Cu use efficiency for grain yield plant^{-1} where cultivar, year, and the cultivar × year interaction effects were all statistically significant (Table 3). For percent Cu use efficiency for grain yield plant^{-1} (Table 5) the main statistical effect was that Oslo had a lower efficiency than the other cultivars.

DISCUSSION

One of the major effects of Cu deficiency in wheat is to cause pollen grain sterility (Graham 1975). In this study, six out of eight test cultivars responded positively with pollen viability improvement after Cu application, confirming the existence of Cu deficiency at this site. This need for a sufficiency of Cu as a requirement for full pollen grain development and viability has also been reported by Graham (1975) and Graham and Pearce (1979) in Australia. The use of starch dye to estimate pollen viability has been justifiably criticized (Jefferies 1977), thus limiting the ability to draw conclusions about pollen viability from the present study. However, the high percent of staining of all tested cultivars did verify that starch was present in the majority of pollen grains and further suggested that the number of functional pollen grains may have been sufficient to induce fertilization without

Table 5. Effects of copper on 1000-kernel weight, number of grains spike^{-1}, and grain yield plant^{-1}, and Cu-efficiency for grain yield of eight Canadian spring wheat cultivars. (Values are means for 2 yrs)

	1000-kernel weight (g)				Number of grains spike^{-1}				Grain yield plant^{-1} (g)		% Cu use efficiency for grain yield plant^{-1}
	Main stems		Tillers		Main stems		Tillers				
Cultivar	−Cu	+Cu	−Cu	+Cu	−Cu	+Cu	−Cu	+Cu	−Cu	+Cu	
Katepwa	35.3	37.5*	33.9	35.3	31.3	32.0	26.9	31.3	5.93	6.85	86.6*ab*
Roblin	35.5	35.2	34.8	32.9	27.5	31.8**	18.9	25.1**	3.18	3.98**	79.9*ab*
Park	31.3	33.2	30.0	30.8	26.7	31.4*	17.0	24.0*	2.93	3.70	79.2*ab*
Laura	32.2	34.2*	30.4	32.1	29.9	37.2	18.8	24.7	2.87	3.87	74.2*ab*
Conway	32.7	36.1*	32.0	32.8	28.1	30.4	21.1	25.3*	4.31	4.79	90.0*a*
Oslo	34.1	36.0*	32.2	31.0	27.0	38.0**	17.7	28.6**	2.75	4.77**	57.7*b*
Columbus	38.1	36.9	35.8	35.9	25.8	27.7	21.7	23.2	3.83	4.63	82.7*ab*
Biggar	34.3	34.0	29.8	29.8	50.5	50.9	37.1	37.6	6.61	6.06	108.4*a*
										LSD (0.05)	34.3
Mean Cu effect		+1.2**		+0.5		+4.1**		+5.1**			+0.70**

a,b For % Cu use efficiency, means with the same letters are not significantly different.

*,** Significant at $P \le 0.05$ and $P \le 0.01$ respectively, for +/− Cu comparisons within cultivars.

causing drastic grain set reduction. Nevertheless, significantly lower numbers of grains spike^{-1} were observed on Roblin, Park and Oslo in the absence of added Cu, particularly on tillers. Thus, it is likely that the limited amount of starch in the pollen grains was not the sole cause of sterility. Graham (1976) suggested that Cu deficiency interferes with the microsporogenesis process at the early booting stage, while Jewell et al. (1988) linked the effects of Cu deficiency on barley to structural defects during the development of anthers and pollen grains. The present study showed that sufficient pollen grains for fertilization were produced from the dehisced anthers. These results do not conform with those of Dell (1981), who suggested that Cu deficiency prevents the anthers of wheat, oats and barley from dehiscing, through a reduced thickening of the endothecial layer of the anthers. Pollen was readily released in the present study.

Six of the eight cultivars tested responded to Cu addition with an increase in percent pollen viability, but only four cultivars (Roblin, Laura, Conway, and Oslo) showed significant response to Cu for percent floret fertility. The quotient that was used to determine floret fertility in the experiment was a function of the number of grains spike^{-1} and the number of florets spike^{-1}. The positive effects of Cu on pollen viability may have accounted for the increase of percent floret fertility of Roblin, Conway, and Oslo, which may have further accounted for an increase in the number of grains spike^{-1}. The influence of Cu on the number of grains spike^{-1} depended on the cultivar, and on the culms assessed. The effects of Cu on the number of grains spike^{-1} were significant on both the main stems and tillers of Roblin, Park and Oslo, while on Conway the influence was only on the production of the grains on the tillers. Responses to Cu are clearly cultivar dependent.

The cultivars tested showed differences in yield potential on Cu-deficient soil, a finding that is consistent with previous reports of genotypically controlled Cu response differences in wheat (Smilde and Henkens 1967; Nambiar 1976; Graham 1984; Graham et al. 1981). Significant effects of Cu clearly indicated the need to supply supplementary Cu to wheat plants at this Stony Plain site. Nevertheless, significant ($P \leq 0.01$) year effects, and interactions with year effects, for grain yield plant^{-1} and yield components also imply that inter-seasonal variation can be influential on the Cu nutrition and consequent productivity of wheat. Variation between years could be accounted for by year-to-year differences in rainfall, which was higher and more evenly distributed in the first year of the trial than in the second year. It has been reported that soil moisture deficit enhances Cu deficiency in wheat by immobilization of Cu into soil lattices (Graham and Nambiar 1981).

Averaged over both years the addition of Cu significantly increased the grain yield plant^{-1} of only two of the eight cultivars (Roblin and Oslo). Biggar showed significantly higher grain yield than the other cultivars and also had the highest percent Cu use efficiency (108.4%). By contrast, Oslo showed the lowest grain yield plant^{-1}, with the lowest Cu use efficiency (57.6%), and responded positively to Cu application with a 73% grain yield plant^{-1} increase. Although Conway showed high efficiency, it was vulnerable to seasonal variations, and performed poorly under the lower rainfall regime of 1991. Chapin (1987) suggested that plants with slower developmental rates have a lower demand for nutrients, and this could be the case for Biggar, a late-maturing cultivar. This hypothesis also seems to hold true for Oslo, which is medium in maturity and very sensitive to Cu deficiency, and for Roblin and Park, which are early-maturing cultivars and perhaps therefore have a higher demand for Cu. Relatively low levels of floret fertility for several of the cultivers in this study, even when Cu-treated, suggest that a higher level of Cu application was necessary to remediate all Cu stress at this site. Trials with higher levels of Cu application would be necessary to confirm this. Significant cultivar × year interaction for percent Cu use efficiency indicated that Cu efficiency of the tested cultivars varied with the year. Seasonally variable responses to Cu application are therefore to be expected.

This field study demonstrated that the effects of Cu deficiency on pollen viability, grain yield plant^{-1}, floret fertility and yield components varied specifically with the cultivar and also with the year of test. Oslo appeared to be the most sensitive to Cu deficiency, whilst Biggar was the most tolerant. Other cultivars were intermediate in Cu efficiency. Sensitivity of the other cultivars depended on the year, and differences between them were more pronounced in the year of lower rainfall.

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