Technical Session II :

Role of Potassium in Plant Physiology

Chloride Requirements for Wheat Production and Leaf Spot Suppression

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Introduction

Potassium chloride is the most common source of potash sold throughout the world, accounting for more than 95 per cent of K consumption. Historically, comparatively little attention was given to the Cl component in this fertilizer. Although Cl has been known to be essential for plant growth since the 1950's (Broyer *et al.*, 1954), for many years it was believed that field-grown crops would not benefit from Cl applications due to its ubiquitous presence in the environment. It was generally assumed that only in greenhouse experiments where nutrients where supplied by manufactured solutions and special precautions (e.g. recrystallization of reagent grade salts; and precipitation of halides with $AgNO_3$) were taken to minimize Cl contamination could deficiency symptoms be produced in plants.

A role for Cl fertilization in crop production was not given serious consideration until research in the Philippines (von Uexkull, 1972), United States and Europe (Russell, 1978), demonstrated yield and / or disease control benefits from Cl. In the North American Great Plains (**Figure 1**), interest in Cl fertilization for wheat began in the mid-1980's and was prompted by two factors. First, winter wheat studies from neighboring regions (i.e. northwestern United States) demonstrated Cl applications increased yield and suppressed take-all root rot disease incited by *Gaeumannomyces graminis* var. *tritici* (Christensen *et al.*, 1981; Taylor *et al.*, 1983). Second, previous studies in the region documented significant yield and quality responses by wheat and barley to KCl on soils with seemingly abundant supplies of available K (Zubriski *et al.*, 1970; Schaff and Skogley, 1982).

In the past 20 years numerous reports and scientific articles have appeared on the role of Cl in wheat production. The potential for yield response and disease suppression in the field to Cl applications has now been well established. In Montana, investigations on the role of Cl in wheat production began in the late 1980's and continued through 1995. This manuscript provides a summary of the more significant observations and results from these studies including information on yield-plant Cl and yield-soil Cl relations, response prediction via plant and soil analysis, Cl fertilizer recommendations, and Cl-deficient leaf spot of wheat.

Description of Study Region

Montana is located within the Great Plains region of North America (**Figure 1**). The climate is predominantly semi-arid with annual rainfall in the wheat growing regions ranging from 300 mm to 450 mm. Rainfall amounts can vary substantially depending upon the proximity to local mountain ranges. Most of the arable land in this region occurs on soils that were once dominated by short-grass prairie. Hard red wheat (spring and winter) is the primary crop grown in this region and production occurs principally (> 90%) under dryland conditions. Summer-fallow (i.e. alternate years of cropping and fallow) is the dominant cropping practice for wheat production. Soils in this region typically test very high in plant available K using traditional ammonium acetate extraction methods. Historically, comparatively little potash was ever applied to the dryland cropped soils of this region because of the high soil K test levels.

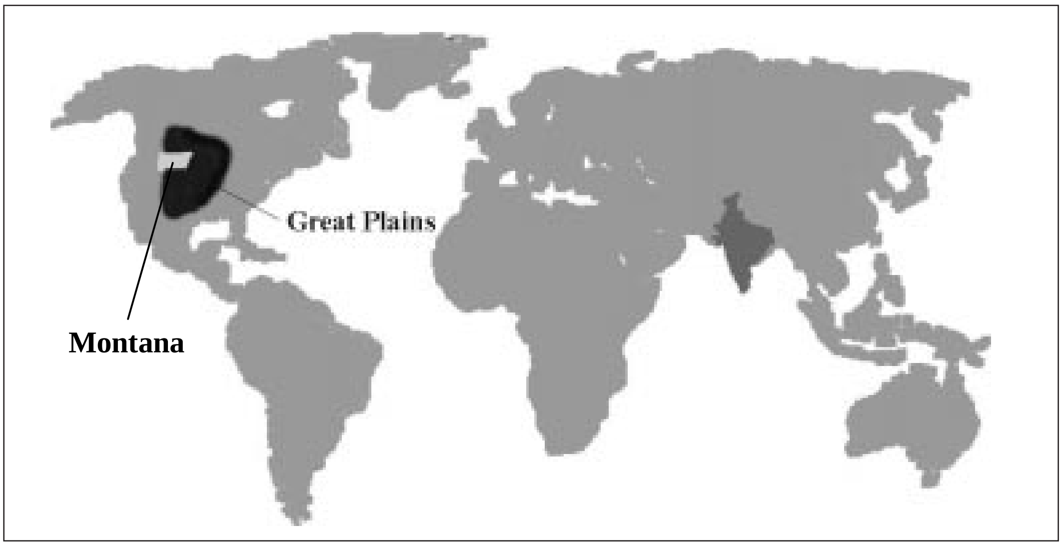

Figure 1. General location of North American Great Plains and Montana (light shaded area)

Field Experiments

Thirty-two field experiments (18 winter wheat, 14 spring wheat) were conducted at 24 sites from 1988 to 1995. The field sites were located on farmer-grower fields and two research center facilities operated by Montana State University. Soil Cl levels were frequently less than 8 kg ha^{-1} in the upper 60 cm of the soil profile. Details on the experimental design have been discussed elsewhere (Engel *et al.*, 1997, 1998, 2001) and are described briefly here. Experiments consisted of multiple cultivar (up to 8 selections) and fertilizer Cl rate investigations. Chloride was applied at two levels, 0 and 67 kg ha^{-1} for winter wheat, 0 and 45 kg ha^{-1} for spring wheat, in the experiments with multiple cultivars. In the fertilizer rate experiments Cl was applied at five levels (0, 11, 22, 45, and 67 kg ha^{-1} for spring wheat; 0, 11, 22, 45, and 90 for winter wheat). Propiconazole fungicide treated and untreated areas were included in several experiments. These comparisons were done in conjunction with an effort to learn more about the origin of Cl-deficient leaf spot syndrome.

Fertilizer KCl was used as the Cl source at all locations except one where granular $CaCl_2$ was used. Fertilizer K_2SO_4 was applied to maintain a uniform rate of applied K. Identical dates of application and placement methods were used for both KCl and K_2SO_4. Sub-surface band applications were used at most locations. At all sites the sulfur variable resulting from using K_2SO_4 was not deemed important due to high indigenous soil SO_4 -S levels. Sufficient fertilizer N and P were applied according to soil test recommendations to ensure an adequate supply of these nutrients.

Soil and plant samples were collected at all field sites. Most frequently, the samples of the whole-plant (above ground portion) were collected at head emergence, or Feekes growth stage (GS) 10.1 (Large, 1954). Plant Cl tissue analyses were performed by the potentiometric titration procedure of LaCroix *et al.* (1970). Soil Cl was extracted with 0.01 M $Ca(NO_3)_2$ using a 2:1 extracting solution to soil (25 g) ratio. Aliquots of the extracts were removed and titrated with 0.005 M $AgNO_3$ as in the plant procedure.

Yield and Plant Cl Relationships

Whole-plant Cl tissue analyses at GS 10.1 can be used to discriminate between sites that are potentially responsive vs. non-responsive to Cl fertilization. Scatter diagrams of relative yield vs. plant Cl (**Figure 2**) provide a compilation of results from 219 cultivar x experiment episodes (147 winter wheat and 72 spring wheat). The relationship expressed in this figure is generally consistent with classic nutrient response curves (Ulrich and Hills, 1967). Three zones of varying Cl status (**Figure 2**) are evident. A deficient or low Cl status zone, plant Cl <1.0 g kg^{-1}, where significant yield responses to applied Cl occurred in 59 of 86 (69%) cultivar x experiment episodes. A critical range or transition zone, plant Cl = 1.0 and < 4 g kg^{-1}, where responses occurred in 25 of 89 (28%) episodes. A zone of adequate Cl status, plant Cl = > 4.0 g kg^{-1}, where significant yield responses occurred in only 2 of 44 cultivar x experimental episodes (<5%).

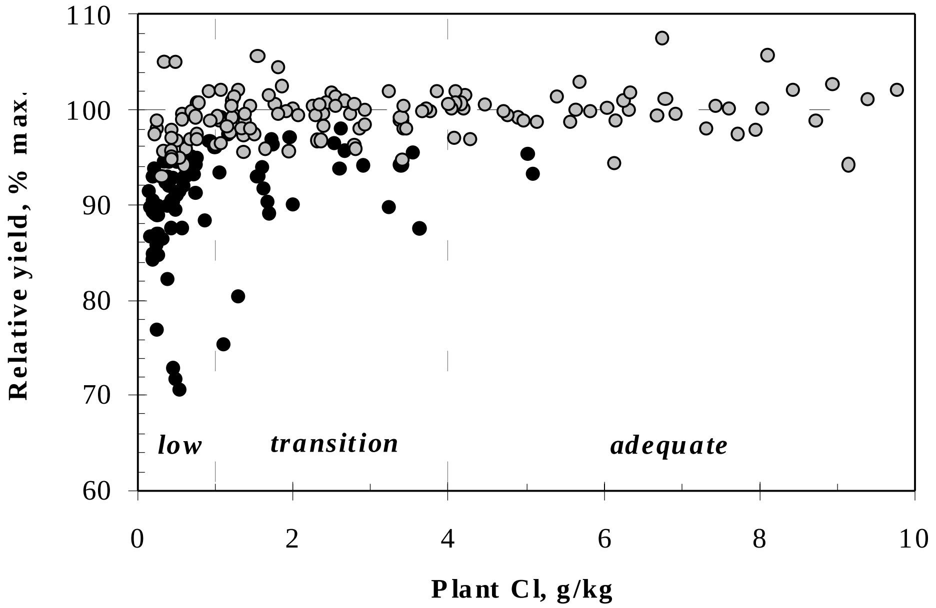

Figure 2. Relative yield (% maximum) vs. whole-plant Cl relationships for wheat in Montana. Cultivar x experiment episodes where Cl fertilization significantly ($P < 0.10$) increased yield are denoted by dark circles. Lighter circles are episodes where Cl fertilization did not increase yield

Grain yield deficits from inadequate Cl in the field are frequently moderate in size even under low Cl status. In this investigation yield increased on an average of 417 kg ha^{-1} (9.7%) in the 86 cases where significant responses to Cl were measured. Hence, relative yield vs. plant Cl relationships (**Figure 2**) do not exhibit the steep drop in yield that is frequently observed in yield curves for other nutrients. The lower limit of plant Cl concentrations observed in these field studies are in the range of 0.15 to 0.20 g kg^{-1}. It is possible yield may drop more precipitously as plant Cl concentrations decrease below this level. Recently, we observed just such a phenomenon in a hydroponic/growth room study (Engel *et al.*, 2001). In this study grain yield of WB881 durum wheat (*Triticum turgidum* L. *var. durum*), was approximately 70% of the maximum at a whole-plant concentration of 0.626 g kg^{-1}, while at a plant Cl concentration of 0.097 g kg^{-1} grain yield was approximately 1% of the maximum.

Biochemical functions of Cl in plants are presumed to require a concentration of no more than 0.10 g kg^{-1} (Fixen, 1993). If correct, the benefits from applied Cl observed in these field studies are more likely due to its osmoregulatory role in the plant (Flowers, 1988). The importance of this function on plant growth and grain yield should be highly dependent on the growing environment (e.g. water and temperature), and other ions that may potentially substitute for Cl in this role. These factors may explain the moderate yield responses to applied Cl, and the broad transition range with its mix of responsive and non-responsive episodes.

Whole-plant Cl concentrations for wheat tend to diminish with time, particularly during the vegetative growth phases. An example of this is illustrated in **Figure 3** for winter wheat. The dropped in tissue concentration is much more pronounced at the higher soil + fertilizer Cl levels. Tissue levels were comparatively stable through the vegetative growth period where Cl fertilizer was not applied (i.e. 3 kg ha^{-1} Cl level). Hence, the nutrient status zones described for wheat at head emergence (**Figure 2**) are not uniformly applicable to samples collected at other growth stages. Given the relative stability of nutrient concentrations under low Cl status it may be easier to identify potentially responsive sites, than sites that are non-responsive

Yield and Soil Cl Relations

Soil Cl content to a depth of 60-cm is generally successful in segregating responsive and non-responsive cultivar x site episodes. Scatter diagrams of relative yield vs. soil Cl (**Figure 4**) reveal a critical soil Cl level of 10 kg ha^{-1} via a Cate-Nelson analysis (Dahnke and Olson, 1990). This method places 73% of the data points in the low Cl-responsive or high Cl non-responsive quadrants, and indicates the soil test is fairly well correlated with response. It is apparent from the figure that the most responsive sites (i.e. yield loss > 10%) had the lowest Cl test levels, but in several cases significant responses were not observed even though soil Cl was below the critical level.

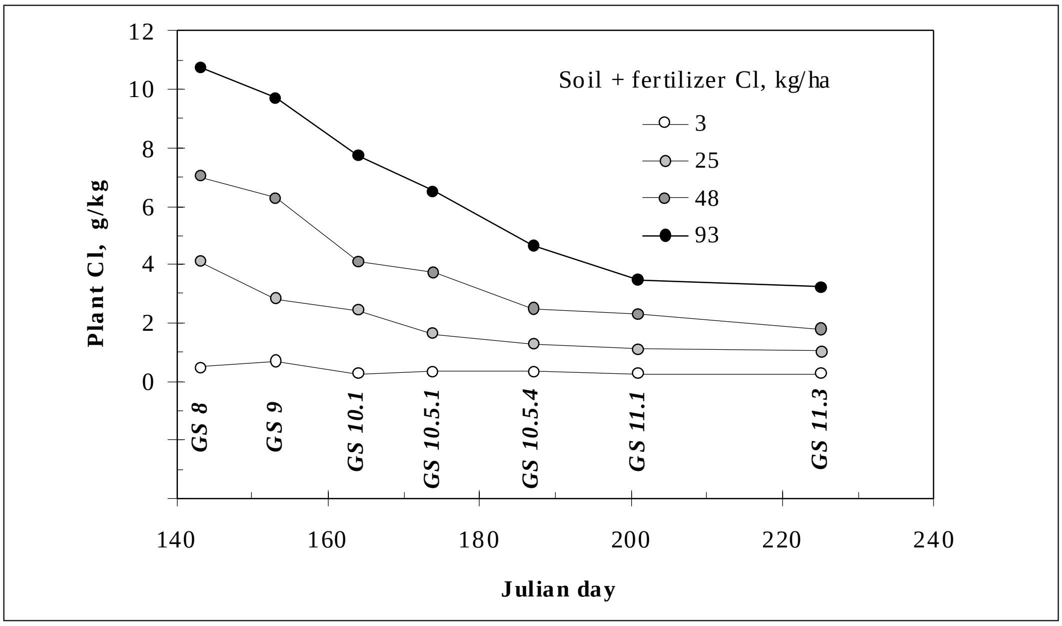

Figure 3. Whole plant Cl vs. time or growth stage (Feekes scale) for 'Redwin' winter wheat. Bighorn Mountain foothills, Montana. 1993. Soil Cl (0-60 cm) = kg ha^{-1}

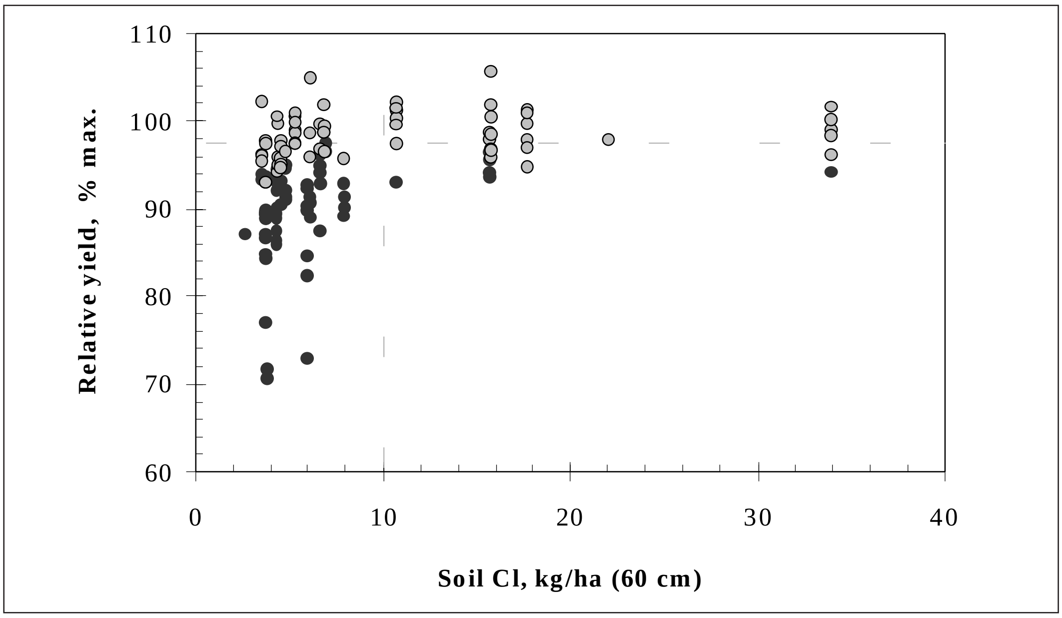

Figure 4. Cate-Nelson analysis of soil Cl content (0- 60 cm depth). 130 wheat cultivar x site episodes in Montana. Control plots only (0 Cl fertilizer). Episodes where Cl fertilization significantly ($P < 0.10$) increased yield are denoted by dark circles. Lighter circles are episodes where Cl fertilization did not increase yield.

Fertilizer Cl Recommendation

Many approaches exist for developing fertilizer recommendations from soil and plant tissue analyses. Generally, recommendations should bring the nutrient concentration in the plant/soil to a level where further increases are not likely to result in improved economic return. Regressing plant Cl concentration on the sum of soil (0-60 cm) plus fertilizer Cl provided some insight into the Cl requirement (**Figure 5**). Chloride concentrations for a given experiment were averaged over all cultivars in this analysis, as cultivar selection did not affect Cl tissue concentrations. In most experiments plant Cl concentrations increased with soil plus fertilizer Cl according to the quadratic relationship expressed by the upper curve. The recommendation suggested by the author is to add sufficient fertilizer Cl to the soil to bring the sum of soil Cl + fertilizer Cl to 30 kg ha^{-1}. This amount of plant available Cl will ensure adequate Cl nutrition as defined by a nutrient concentration of 4.0 g kg^{-1}, or the upper end of the transition range (**Figure 2**).

The upper end of the plant Cl transition range was chosen in the proposed guideline, because of the modest cost of Cl applications and the potential for carryover from one season to the next in semi-arid wheat growing areas such

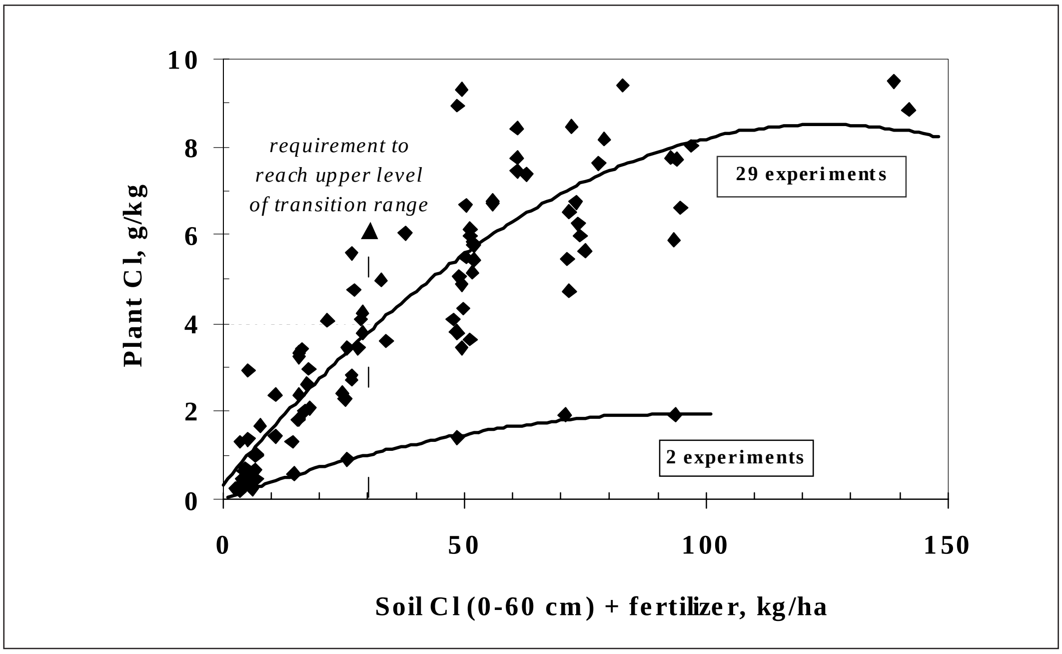

Figure 5. Regression relationship of plant chloride content on sum of soil (0-60 cm) plus fertilizer chloride for wheat in Montana, USA

as Montana. Chloride fertilizer, most frequently sold as granular KCl (0-0-62 or 0-0-60), is priced at \$0.35 kg^{-1} (U.S. dollars). Therefore, the material cost of a 25 kg ha^{-1} Cl application is \$8.75 ha^{-1}, and a 60 kg ha^{-1} yield response would cover this expense at a grain price of \$147 Mg^{-1}. In addition, only small quantities of applied Cl (< 3 kg ha^{-1}) are translocated to the grain, and therefore removed from a site at harvest (**Table 1**). A large fraction of the Cl absorbed by wheat is found in the straw. This Cl should be recycled or released to the soil as the residue decomposes. As rainfall is comparatively low in many important North American wheat-growing areas, leaching events are infrequent even though Cl is mobile in the soil. In this investigation, only at two experiments was there evidence of significant fertilizer Cl losses (lower curve, **Figure 6**). This was believed to have resulted from high precipitation (rain and snow) received during the fall and winter months.

Table 1. Chloride distribution in Redwin winter wheat at physiological maturity. Bighorn Mountain foothills, Montana. U.S.A. 1993.†

Fertilizer Cl‡	*Grain yield*	*Straw Cl*	*Grain Cl*	*Total Cl*
kg ha^{-1}	kg ha^{-1}	------------------------ kg ha^{-1} ------------------------		
0	4099	3.1	1.5	4.6
22.5	4744	18.1	2.7	20.8
45	4791	28.7	2.6	31.3
90	4589	54.3	2.6	56.9
LSD(.05)	430	15.3	0.4	15.7

†Soil Cl (0-60 cm depth) = 3.0 kg ha^{-1}
‡Fertilizer Cl applied as KCl

Chloride Deficient Leaf Spot

A peculiar leaf spot complex of wheat that results in tissue necrosis and yield losses is sometimes observed in the North American Great Plains and northwestern United States. Symptoms may be confused with tansport (incited by *Pyrenophora tritici* f. sp. *repentis*). Experiences in Montana indicate that lesions first become visible at flag leaf emergence to late boot stage. Symptoms initially appear on the lower leaves (e.g. flag-2 & flag-3) then progress to the younger leaves after they became fully emerged. Lesions initially appear as small (1 to 3 mm across) circular to oblong chlorotic spots. Later, the chlorotic affected areas become necrotic. In the field, leaf spot severity (percentage of leaf blade tissue affected by chlorotic or necrotic lesions) frequently increases up through early grain-fill. Historically, plant pathologists and breeders have referred to this phenomenon as a *physiological leaf spot of wheat* (Wiese, 1977) because it was presumed to result from an unknown metabolic process, or genetic dysfunction, rather than an infectious pathogen.

Conclusions from Montana field studies (1992-1995) indicated this phenomenon resulted from inadequate Cl nutrition and the term *chloride-deficient leaf spot syndrome of wheat* was proposed to describe it (Engel *et al.*, 1997). This conclusion was based on a number of considerations. First, absence of evidence indicating an infectious organism(s) was responsible for the appearance of lesions. Specifically, foliar fungicide applications (i.e. propiconazole) had no effect on leaf spot severity, and attempts to isolate fungi from affected tissue proved negative. Second, damage in susceptible cultivars was closely linked to plant Cl levels (**Figure 6**). Leaf spot damage in susceptible cultivars was minimal = ?1.0 g kg^{-1} plant Cl. Leaf spot damage increased exponentially as plant Cl levels dropped below a 1.0 g kg^{-1} threshold level. Third, small applications of Cl fertilizers prevented the appearance of leaf spot symptoms. The soil (0-60 cm) + fertilizer requirement for leaf spot control was generally < 30 kg ha^{-1} (**Figure 7**). In addition, recent growth room investigations indicate leaf spot symptoms can be reproduced in hydroponic culture by with holding Cl from nutrient starter and refill solutions (Engel *et al.*, 2001).

Appearance of Cl-deficient leaf spot of wheat has been found to be very cultivar specific in the field. This means that at a low Cl testing site (i.e. < 10

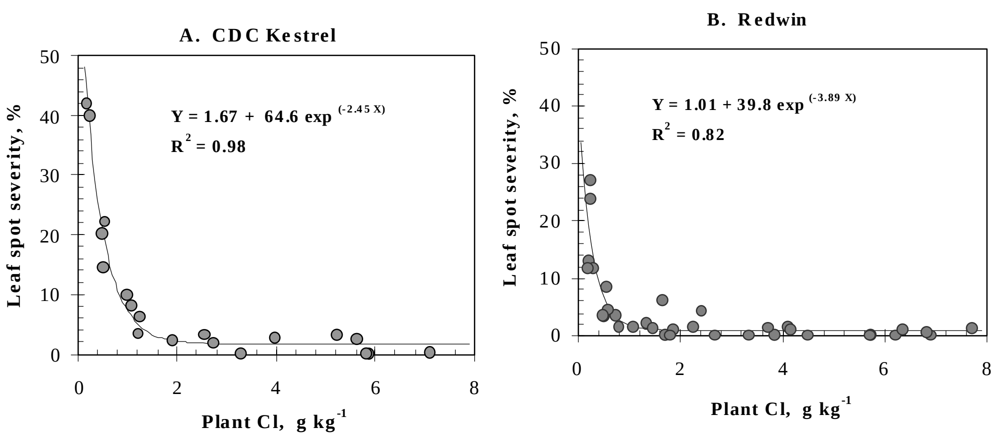

Figure 6. Flag leaf spot severity of CDC Kestrel (A) and Redwin (B) winter wheat as affected by whole-plant Cl. Montana.

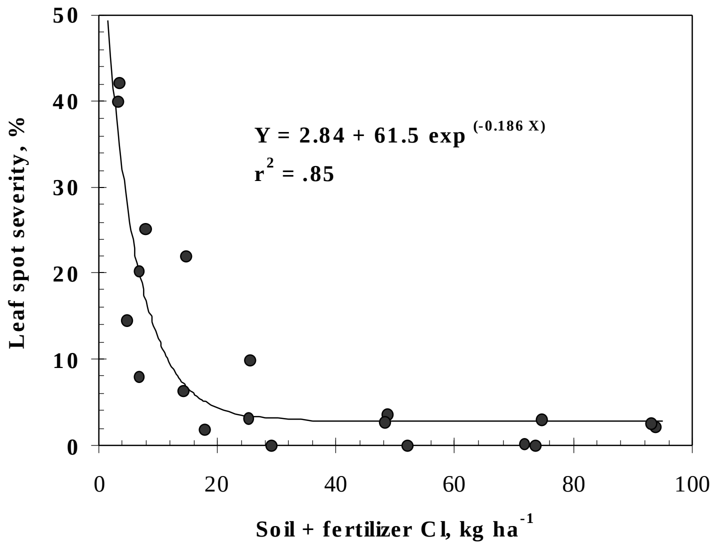

Figure 7. Flag leaf spot severity of CDC Kestrel winter wheat as affected by soil (0-60 cm) plus fertilizer Cl in Montana

kg ha^{-1}), selected cultivars produced lesions while others do not. Among cultivars that produce lesions, leaf spot severity can vary greatly. High moisture conditions during the vegetative growth phases appear to enhance the formation of lesions. Hydroponic/growth room studies indicate cultivar susceptibility to leaf spot cannot be traced to differences in Cl uptake, or concentration in specific plant parts (i.e. leaf blades, tops, roots). Halide ion substitution studies reveal Br does not substitute for Cl's role in leaf spot suppression, but rather aggravates damage from leaf spotting (Engel *et al.*, 2001). This is significant because early investigators found Br additions to low Cl hydroponic mediums would prevent or reduce the severity of Cl deficiency in sugarbeet (*Beta vulgaris*) (Ulrich and Ohki, 1956) and tomato (*Lycopersicon esculentum*) (Ozanne *et al.*, 1957), respectively. Hence, the physiologic processes responsible for the appearance of Cl-deficient lesions in wheat are probably different than processes responsible for the appearance of chlorosis and necrosis in tomatoes and sugarbeets.

While the physiologic process(es) responsible for the appearance of lesions are unknown, electron microscopy of thin sections indicates structural differences between leaf mesophyll cells from healthy and affected tissue (Engel *et al.*, 1997). In healthy tissue, chloroplasts are packed tightly against the plasmalemma. The central vacuole is well hydrated and occupies the majority of the cell volume (**Figure 8A**), a characteristic of mature cells (Maas, 1986). In lesion-affected tissue the chloroplasts are no longer organized against the plasmalemma and the central vacuole occupies a comparatively small fraction of the cell volume. Chloroplasts may be swollen and the grana stacks are not as tightly packed. In several cases the chloroplast envelope is no longer visible, perhaps having burst and allowing thylakoid fragments and grana stacks to spill into the cytoplasm (**Figure 8B**)

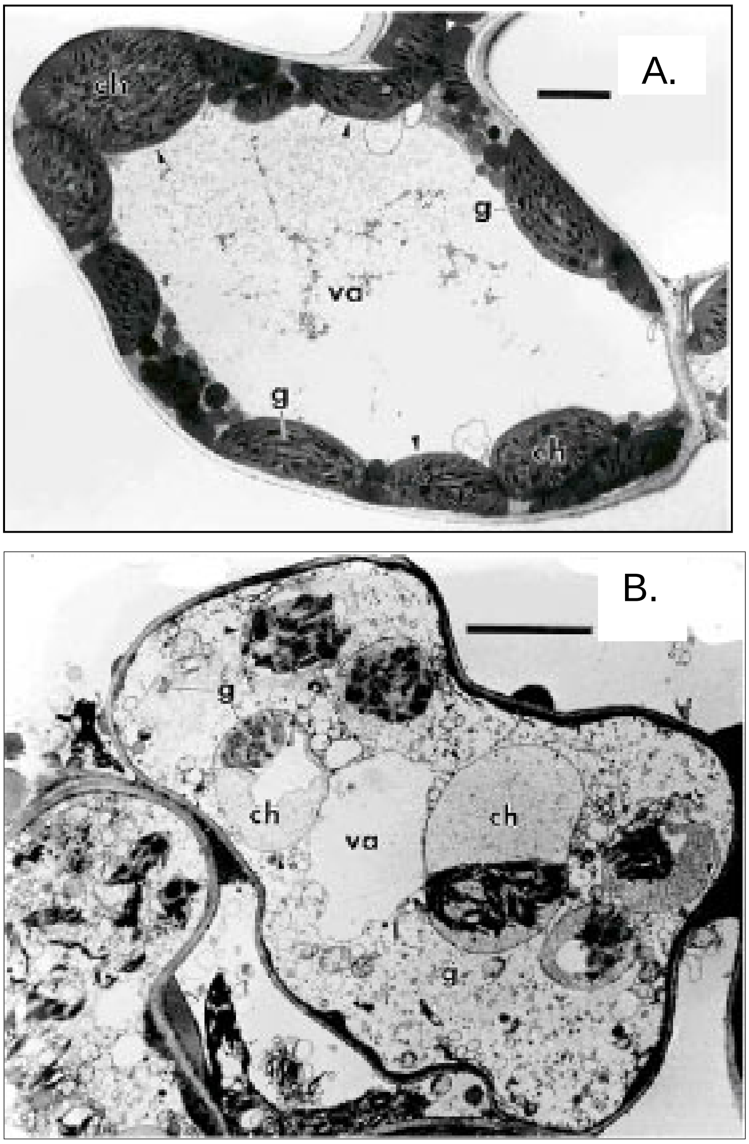

Figure 8. Cross-section of mesophyll cells from healthy (A) and necrotic (B) tissue of Redwin winter wheat flag leaves showing chloroplasts (ch), central vacuole (va), chloroplast envelope (arrowheads), and grana stacks (g). Bar is 4.0 µm.

Conclusions

Research studies conducted in Montana indicate that wheat yield losses due to inadequate Cl nutrition occur in the field. Plant and soil analyses are diagnostic tools for identifying responsive and non-responsive sites to Cl fertilization. Whole-plant Cl concentrations at head emergence < 1.0 g kg^{-1} are indicative of Cl deficiency and respond to applied Cl at a 69% frequency. Response frequency to applied Cl diminishes to 28% where whole-plant Cl is = 1.0 and < 4 g kg^{-1}. Whole-plant Cl concentrations = 4 g kg^{-1} are associated with adequate Cl nutrition. A soil Cl level (0-60 cm) of 10 kg ha^{-1} is critical for wheat. The fertilizer recommendation for maximum yield is to apply sufficient Cl such that soil (0-60 cm) + fertilizer Cl equals at least 30 kg ha^{-1}. Chloride-deficient leaf spot is found to occur at sites where whole-plant Cl falls below a 1.0 g kg^{-1} threshold level. This phenomenon is very cultivar specific, and not all wheat cultivars are susceptible in the field. Leaf spotting in susceptible cultivars is prevented by application of Cl fertilizers (soil + fertilizer = 30 kg ha^{-1}). Leaf spot occurrence and severity in the absence of adequate Cl is enhanced by high moisture, or conditions that promote lush vegetative growth. This requires further investigation, as do the physiological processes responsible for lesion formation.

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