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Temporary Nutrient Deficiency - A Difficult Case for Diagnosis and Prognosis by Plant Analysis

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ABSTRACT

Plant analysis aims to either detect deficiency at the time of sampling (diagnosis) or predict its occurrence at a later stage of growth (prognosis). Its use is based on the presumption that the plant nutrient status will either be constant with plant age or follow a predictable pattern of change over time after sampling. However, a period of deficiency during plant growth followed by the recovery of nutrient uptake to satisfactory rates may cause an irreversible impairment of growth which plant analysis fails to diagnose or predict. Several cases are considered1 each involving a temporary deficiency of, or interruption to nutrient supply. Such cases generally involve but are not restricted to micronutrient deficiency. For example, B deficiency impairs early seedling growth when seeds low in B is planted, even on El fertilised soils. Low B concentration in seeds diagnoses the subsequent impairment of seed germination or seedling establishment: however, leaf analysis after emergence does not. Similarly, Zn deficiency impairs early growth of transplanted oilseed rape *(Brassica napus* L.) seedlings and eventually depresses seed yield. However, leaf analysis during crop growth fails to diagnose a Zn deficiency. Finally, temporary B deficiency induced by low vapour pressure deficit or low soil water especially during reproductive development may depress yield markedly but remain difficult to diagnose by plant analysis. Strategies for diagnosing and predicting such temporary deficiencies are discussed including the measurement of environmental parameters such as pan evaporation or rainfall and their inclusion in multi-variate regression models of plant response to nutrients.

INTRODUCTION

Smith and Loneragan (1997) pointed out that environmental factors which induce intermittent symptoms of nutrient disorders may confuse the interpretation of plant analysis. However, there has been relatively little further consideration given to this phenomenon and its implications for plant analysis or to the alternative strategies required to diagnose or predict a nutrient disorder in these circumstances. The essence of the problem is that a period of deficiency during plant growth followed by the recovery of nutrient status to levels satisfactory for unrestricted growth may cause an irreversible impairment of yield potential which plant analysis fails to diagnose or predict. Such cases of temporary nutrient deficiency fall into four main categories: an increase in functional nutrient requirement occasioned by changed environmental conditions; low nutrient concentrations in planting seed; low nutrient content in other planting stock such as transplanted seedlings; and impaired nutrient supply or

uptake during crop growth followed by a subsequent recovery. Temporary nutrient deficiencies are most common with nutrients which are phloem immobile and those that are immobile in the soil under the growth conditions experienced. Understanding the nature of these temporary nutrient deficiencies and their implications for the failure of plant analysis to diagnose or predict deficiencies will ultimately lead to more reliable outcomes from plant analysis. in the present paper, results of recent studies, mostly with micronutrients, are examined for their insight into the phenomenon of temporary nutrient deficiencies. The aim of the paper is to determine strategies for improving the efficacy of plant analysis in cases where a temporary nutrient deficiency can be expected.

The implications of temporary nutrient deficiency need to be considered separately depending on whether plant analysis is used for diagnosis or for prognosis. Plant analysis is used to diagnose a deficiency existing in a crop at the time of sampling (Smith and Loneragan, 1997). When critical concentrations for diagnosis are established in defined plant parts by determining the functional nutrient requirement or using precautions to avoid rapid nutrient depletion in the growth medium, this value should in principle be a constant value which defines the unique requirement for that nutrient for physiological and biochemical functions (Smith and Loneragan, 1997). However, where changes in ambient conditions alter the form, function or distribution of the nutrient, a change in the functional nutrient requirement is possible even though few such cases have been convincingly demonstrated. There are suggestions that high light intensity accentuates deficiency symptoms of boron (B), potassium (K), magnesium (Mg) and zinc (Zn) (Marschner and Cakrnak, 1989; Shorrocks, 1997) and that low temperature increases the intensity of symptoms of B deficiency (Bell, 1997; Shorrocks, 1997). Diagnosis of nutrient deficiency by plant analysis may fail when sampling occurs after recovery of plants from a period of deficiency: in such cases plant analysis may detect differences in nutrient concentrations in sampled plant parts which are correlated with, but not causally related to, the impaired growth.

Plant analysis is also used, along with soil analysis to predict the future occurrence of a nutrient deficiency (Smith and Loneragan, 1997). Prognosis is based on certain presumptions about the pattern of change in nutrient concentrations in plants and soil nutrient supply over time. When the presumptions about the pattern of change in nutrient concentrations over time are not valid, plant analysis may fail to predict a nutrient disorder. The key factors that need to be assessed by a plant test for prognosis are information on: nutrient stores available for redistribution within the plant; nutrient supply over time from the soil; and the nutrient requirements for growth and yield (Smith and Loneragan, 1997). Thus temporary nutrient deficiency is most common firstly with phloem-immobile nutrients where retranslocation of stored nutrient reserves is not sufficient to compensate for a decline in external nutrient supply. Secondly, dry soil conditions or low vapour pressure deficit which can occur temporarily during any stage of crop development may interrupt the supply of nutrients from the soil. And finally, temporary nutrient deficiency is most prevalent with nutrients required specifically for particular stages of crop development such as secondary swelling of roots (Halbrooks and Peterson, 1986), pollen development or seed set (Dell and Huang, 1997).

Temporary Changes in Functional Nutrient Requirements for Diagnosis

Many reports suggest that critical concentrations for diagnosis vary as a result of interactions with other nutrients and environmental factors. However, few of these reports actually deal with diagnosis, and of those that do, fewer still have compelling evidence for a change in the functional nutrient requirement (Smith and Loneragan, 1997). Most reports of interactions with other nutrients and environmental factors are actually concerned with prognosis and these will be discussed below. Thus there are relatively few known factors which can potentially induce a temporary deficiency by increasing the functional nutrient requirement.

While high light intensity has been reported to accentuate deficiency symptoms of K, Mg and Zn (Cakmak and Marschner, 1989) it is not clear whether there was also an increase in the functional nutrient requirement. However, high light intensity does appear to increase the functional B requirements of plants for leaf elongation and for membrane permeability. In a glasshouse study with black gram *(Vigna mungo* L. Hepper), shading of plants which reduced light intensity from 70 to 35 % of full sunlight decreased the B concentration required in youngest open leaves for unrestricted leaf blade elongation from 15 to 10 mg kg^{-1} (Noppakoonwong et al., 1993). Thus the internal B requirement for leaf expansion appeared to decrease when the leaf was exposed to reduced light intensity. Short term exposure to high light intensity also increases the rate of K leakage from leaf cells of low B sunflower plants *(Helianihus annuus* L.) (Cakmak et al., 1995). None of these previous studies have answered the central question: whether high light intensity or long photoperiod increases the internal B requirement. Physiological and biochemical mechanisms by which light intensity and 13 deficiency interact in plants remain unknown. Cakmak and Romheld (1997) favoured the hypothesis that high light increases the internal requirement for B to prevent photo-oxidative damage of membranes by free radicles and phenol but more evidence tends to discount this possibility (Pfeffer et al., 1998). The field significance of these findings for the diagnosis of B deficiency remain unclear. Short term fluctuations in light intensity have the potential to alter the sensitivity of crops to B deficiency but this needs to be better understood at a mechanistic level and also in terms of light regimes that increase the risk of plants to B deficiency. Similarly, the possibility that high light intensity increases internal requirements for K, Mg and Zn also needs further examination.

Several reports have linked low temperature damage in plants and B deficiency (Shorrocks, 1997). Boron foliar sprays have been reported to alleviate symptoms of B deficiency in a range of trees and fruit trees exposed to low temperature. Whilst most of the low temperature studies involved plants exposed to frost, Hanson and Breen *(1985)* reported that autumn foliar sprays of B increased fruit set of prunes *(Prunus domestica)* during a spring with a mean temperature of 8°C (and no frost) but not in a warm spring (mean temperature of 12°C). The significance of these reports for the diagnosis of B deficiency are still unclear because as yet no evidence of an increase in functional B requirements with low temperatures has been demonstrated. Experimental evidence that low temperatures increase sensitivity to B deficiency *is* limited to one brief report by Parr and Loughman (1983) who examined the

response of P uptake by maize *(Zea mays)* to decreasing temperature in the presence or absence of B in solution. In solutions supplied with B, the uptake of P declined with decreasing temperature but below 20°C there was a distinct inflection in the curve implying a temperature dependent change in membrane conformation from a fluid to a gel state. That low temperature causes a change in membrane properties has been reported previously (Simons, 1974). What had not been previously reported were the findings of Parr arid Loughman (1983) that the critical temperature at which membrane properties changed, depressing P uptake, was 2°C higher in B deficient solutions than in B adequate solutions. These results, limited though they are, imply that the low B tissues might be more sensitive to cold temperature damage to membranes than B adequate tissues. However, it is still unclear whether the functional B requirements increase with periods of low temperature.

Temporary Nutrient Deficiency and Its Prognosis by Plant Analysis

The problems of temporary nutrient deficiencies for the prediction of the consequences of the disorder are threefold: firstly, such periods of temporary deficiency are difficult to predict; secondly, leaf analysis after the event gives no indication of the cause of the loss of yield potential which occurs during the period of deficiency, and; thirdly, not all periods of deficiency cause an irreversible loss of yield potential. Three cases of temporary nutrient deficiency and their implications for prediction of nutrient deficiency will be considered: low nutrient concentrations in planting seed; low nutrient content in other planting stock such as transplanted seedlings; and impaired nutrient supply or uptake during crop growth followed by a subsequent recovery.

Low Seed Nutrient Concentrations

Low seed nutrient concentrations can cause a temporary deficiency in nutrient supply for the developing seedling which directly impairs early crop growth but only for perhaps a few days. However, the consequences of this temporary deficiency continue to limit yield potential often until final harvest. There are numerous cases of low seed nutrient concentrations depressing the subsequent growth of plants, leading to depressed seed yield: boron (Bell et al., 1989; Rerkasem et al., 1990, 1997); calcium (Cox et al., 1976); manganese (Crosbie et al., 1993; Marcar and Graham, 1986), phosphorus (Bolland and Baker, 1989; Ros et at., 1997a; Thomson et al, 1992) and zinc (Grewal arid Graham, 1997; Rengel and Graham, 1995a,b).

Extremely tow nutrient concentrations depress seed viability by damaging the seed embryo at some stage during its development or soon after imbibition (Bell et at., 1989; Cox et at., 1976; Crosbie et at., 1993), For example, Bell et al. (1989) showed that seed B concentrations <6 mg B kg^{-1} in black gram (*Vigna mungo* L. Hepper) strongly increased the percentage of non-viable seeds and the percentage of viable seeds which produced abnormal seedlings. Soybean *(Glycine max* L. Merr.) seed containing 7-10 mg B kg^{-1} or less had decreased germination and seedling emergence in sand culture (Rerkasem et al., 1997). Such cases of nutrient deficiency in the seeds themselves can be diagnosed by plant analysis but as Smith

and Loneragan (1997) note, cannot be corrected by treatment of the seed during or after germination. Moreover, their implications for yield potential cannot be detected by plant analysis after sowing. Yet the decline in seed viability caused by low seed B or Mn concentration may greatly decrease crop yield potential by reducing crop stand density (Bell et al., 1989; Crosbie et at., 1993). Diagnosis of the deficiency by analysis of the seed before sowing allows the seeding rate to be increased to compensate for decreased seed viability.

Low Ca and low Mn, like low B, have been reported to decrease seed viability (Cox et at., 1976; Crosbie et at., 1993). In lupin *(Lupinus angustifolius* L.), seed viability as measured by tetrazolium staining was decreased by one-third in seed containing 7 mg Mn kg^{-1} compared to those containing 35 mg Mn kg^{-1} (Crosbie et al., 1993). In wheat *(Triticum aestivum* L.), seed Zn concentrations *<5-10* mg kg^{-1} depress seed germination (Al-Samerria, 1984), whereas in oilseed rape *(Brassica napus* L.) seed Zn concentration of 22-28 mg kg^{-1} did not (Grewal and Graham, 1997). By contrast, low P concentration in seed does not appear to directly affect seed viability (Harrington. 1960).

At moderately low seed B concentrations, the effects on subsequent crop growth are not on seed viability but rather on seedling vigour (Rerkasem et al., 1993, 1997; Smith et al., 1992). Unlike the decrease in seed viability in low B seed which cannot be corrected by increased external B supply, the vigour of the germinated seedlings is responsive to the soil B supply (Table 1: Rerkasem et at., 1990, 1997). That is, low seedling vigour from low B planting seed can be alleviated in part or fully by increasing soil 13 supply. In soybean, seed containing B in the concentration range 10-20 mg B kg^{-1} produced abnormal seedlings on low B soils. However, B concentration in the youngest fully expanded leaf at early flowering did not respond to the seed B treatments. Thus, plant B analysis at early flowering while predicting the seed yield response to soil B levels would have failed to detect the effects of low seed *B* on subsequent yield. Rerkasem et al. (1997) suggested that the effects of low seed B were to restrict early growth rather than to cause a deficiency in the plant at maturity. Thus when sampled at early flowering, the soybean plants grown from low B seed had an internal B status determined by the soil B levels not by the B concentration of the planting seed. However, because the low B in the seed decreased seedling vigour, it had a lasting impact on the yield potential of the crop by restricting the number of pod bearing nodes and pods per plant and to a lesser extent the number of seeds per pod. By contrast, seed size which is the last of the yield components to be affected potentially by B deficiency was not depressed by low B in the planting seed.

Low P concentration in seeds of a range of legume *(Trifolium balansae,* Bolland and Baker, *1989; Lupinus angustifolius,* Holland et al, 1989, Thomson *et* al, 1992; *Medicago polymorpha,* Bolland and Baker 1988; *Trifolium subterranean,* Bolland and Baker, 1989) and cereals species *(Oryza saliva,* Ros et al., 1997a; *Triticum aestivum,* Holland and Baker, 1988) depresses early seedling growth after germination. Yield was also depressed by sowing low P seed. However, the direct effects of low P concentration in planting seed on seedling growth appear to be relatively short-lived. In lupin, the depression in relative growth rate of seedlings from low P planting seed had disappeared by 6-9 days after seed imbibition except in low P

TABLE 1. Effects of soil boron (B) supply on a low B silty loam soil from northern Thailand on the percentage of normal soybean seedlings which emerged from planting seed with increasing B concentrations. Values are means at 21 days after sowing of four replicates ± SE. From Rerkasem et al. (1997).

Soil B treatment	Seed B concentration (mg kg^{-1})		
	7	10	23
-B	7±1	8±1	79±11
+B	14±1	66±8	83±12

soil (Thomson et al, 1992). Similarly in rice, high seed P concentrations stimulated relative growth rate of germinated seedlings during the first 10 days after sowing, but not during the subsequent 20 days (Fig. 1). Nevertheless, the initial depression in relative growth rate caused by sowing low *P* seed had persistent effects on dry matter production in both lupin and rice, especially in low *P* soil. While P concentrations in shoot, youngest emerged blade and shoot tips all responded to increasing P concentration in planting seed, they were of no diagnostic value (Ros et al., 1997a).

Low Zn depresses seedling vigour in wheat and oilseed rape (Rengel and Graham, 1995a; Grewal and Graham, 1997) and has been reported to depress grain yield in the former species (Rengel and Graham, 1995b). Like low P in seed, low Zn in planting seed limits seedling growth most severely when the soil is also low in Zn supply. However, the seed Zn response is more complex than that of the seed P response because the early seedling growth of Zn efficient cultivars is less sensitive to low seed Zn concentration than that of Zn inefficient cultivars (Grewal and Graham, 1997). At 2 weeks after sowing, shoot Zn concentrations reflected differences in seedling growth of oilseed rape seedlings suggesting that plant analysis might diagnose Zn deficiency caused by sowing low Zn seed on low Zn soil. However, 6 weeks after sowing, Zn concentrations in plant parts did not vary amongst plants from high and low Zn planting seed, or among three cultivars of different Zn efficiency. At this time plant analysis was unable to diagnose the substantial differences in plant growth induced by high and low Zn planting seed of three oilseed rape cultivars.

Low molybdenum (Mo) in seed depresses subsequent growth of plants but in some cases it is a response to Mo content in the seed, and in others to Mo concentration. At one extreme, high Mo content in a seed is sufficient to supply all the plant's needs for Mo to maturity (Harris et al., 1965). Thus on low Mo soil, high Mo content in the seed may replace the need for Mo fertiliser. However, at low Mo concentrations in seed, abnormal seedlings of maize developed and their field emergence was depressed (Weir and Hudson, 1966). As with low seed B, low Mo in seed may be diagnosed by analysis of seed before sowing and a high Mo seed source substituted, or the seeding rate adjusted accordingly. In the legume black gram,
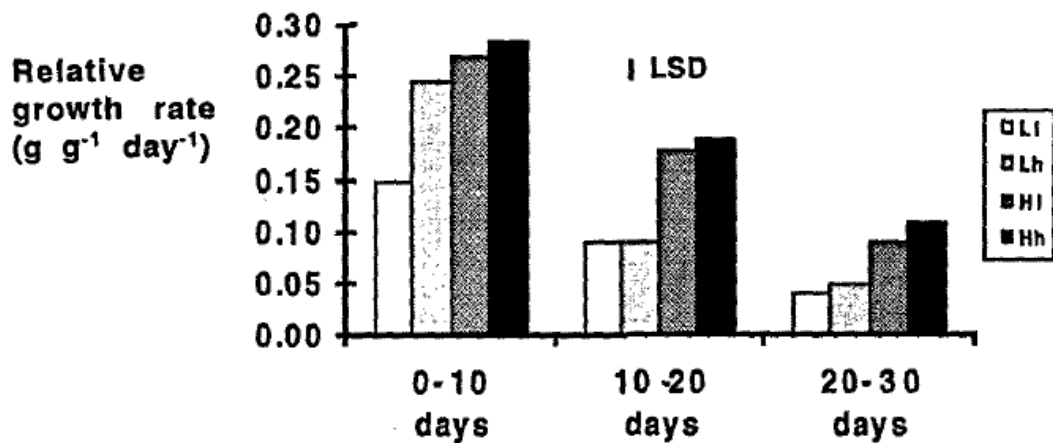
FIGURE 1. Effect of high (h, 0.24% P) and low (1, 0.115% P) seed P on relative growth rate of shoots (g g^{-1} day1) of rice cv. IR66 during the periods, 0-10, 10-20 and 20-30 days after sowing in a sandy soil treated with high (H, 150 mg K$_2$HPO$_4$ kg^{-1} soil) and low (L, zero added P) soil P. Adapted from Ros et al. (1997a). The vertical bar represents the LSD (P <0.05).

low Mo concentration in seed may depress early nodulation (Jongruaysup et at., 1993). When low Mo seed was sown, shoot Mo in black gram declined to <22 ng g^{-1} between 9 and 15 days after sowing and hence plant analysis at this time would have diagnosed Mo deficiency. However, 18 days after sowing shoot Mo concentrations recovered to > 22 ng g^{-1} and were no longer diagnosed as Mo deficient but nodule mass and nodule function continued to be depressed relative to that in plants from high Mo seed.

Low Nutrient Uptake by Planting Stock

A number of field crops and horticultural crops are established by transplanting seedlings raised in nursery seedbeds. Apart from rice, other transplanted field crops include oilseed rape and cotton in parts of central China, and tobacco and tomato in eastern USA (Reed, 1998). Thus in a range of farming systems, temporary nutrient deficiency in transplanted seedlings may be limiting yield potential of crops. Recent research suggests that transplanted oilseed rape has a higher external Zn requirement for early plant growth than direct sown plants on the same soil (Mulyati et at., 1997). The nature of the increased responsiveness of transplanted oilseed rape seedlings to Zn suggests that a temporary Zn deficiency impaired seedling growth during recovery from transplanting. Following recovery of seedlings from transplanting, there was no evidence that plants remained Zn deficient, but growth potential continued to be limited leading to depressed seed yield. These findings help to explain the previous reports from field experiments in China where Zn responses in oilseed rape were prevalent but the pattern of response was puzzling (Hu et al., 1996). In China, the transplanted oilseed rape seedlings responded strongly to fertiliser Zn during the rosette stage about 2 months after transplanting, but with time the relative response to Zn diminished (Fig. 2). At harvest, the magnitude of the response was equivalent to 7-18 % increase in seed yield,

but was remarkably consistent despite differences in soil type, extractable DTPA-Zn levels and seasons. Secondly, when leaf samples were taken from the crops at rosette and green bud stages they invariably contained adequate Zn concentrations and were not well correlated with the growth responses to Zn. Thus leaf analysis failed to diagnose any Zn deficiency in transplanted oilseed rape. Moreover, there was no relationship between leaf Zn at rosette or green bud stages and seed yield from which a critical value for prediction of Zn deficiency could be derived. By contrast, Grewal and Graham (personal communication) have obtained close relationships between seed yield in canola and leaf Zn concentrations of direct sown crops in southern Australia from which tentative critical concentrations of 17-19mg Zn kg^{-1} were derived for the youngest mature leaf at stem elongation stage.

Low P supply to tomato seedlings in seedbeds depressed yield potential by *50%* (Menary, 1967). Similarly, low P supply in the seedbed for rice has been shown to depress post-transplanting growth in the mainfield, leading to depressed grain yield (Ros et al., 1997b). Plant analysis of samples collected after transplanting will probably not diagnose these deficiencies neither can they predict the deficiency *post-priori*. Plant analysis will be limited to detection of low nutrient concentrations in seedlings before transplanting, However, few critical concentrations exist for diagnosis *of* nutrient deficiency in seedlings prior to transplanting.

Environment x Nutrient Interactions

Critical concentrations for the prediction of nutrient deficiencies are derived from relationships between growth and leaf nutrient concentrations which assume ideal conditions for the realisation of yield potential for a particular environment. It is recognised that factors like disease, weeds, waterlogging, restricted root growth or deficiency of other nutrients will limit the realisation of yield potential in a particular season and therefore may invalidate the relationship. Indeed it is often recommended that leaf sampling be postponed when plants are suffering drought or other evident stresses (Smith and Loneragan, 1997).

Those environmental factors that depress the uptake of nutrients disproportionately to their direct effects on plant growth will alter the probability of deficiency. However, because environmental factors such as low soil water, low temperature, and low vapour pressure deficit act intermittently, or temporarily during the growing season, they are difficult to predict. When the pattern of change in leaf nutrient concentrations induced by unusual environmental conditions does not follow the normal pattern on which the critical values are predicated, the normal critical values may not apply in those unusual conditions.
An added complexity in the effects of environmental factors is the timing of the temporary deficiency, and its duration. Halbrooks and Peterson (1986), for example, showed that withdrawal of external B supply from table beet *(Bela vulgaris* L.) for 6 or 9 days at 20 days after the appearance of the first pair of true leaves induced the development of the blackheart symptoms in roots, but withdrawal of external B supply for only 3 days did not. By contrast, earlier or later periods of withdrawing B supply did not induce any blackheart symptoms. The
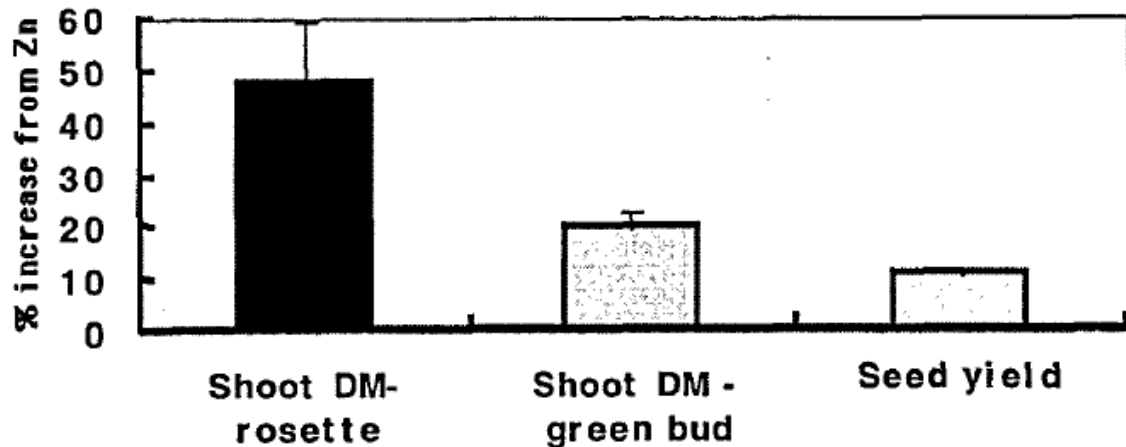
FiGURE 2. The decline with plant age in relative response of shoot dry matter (DM) and seed yield to zinc (Zn) in transplanted oilseed rape grown with or without Zn fertiliser in Hubei province, PR China in 1992-95. Values are means ± SE from nine field experiments where the increase in shoot DM or seed yield with Zn added in each experiment was calculated as a percentage of that without Zn added. From Hu et al. (1996) and Lu Zhonggui (personal communication).

development of blackheart symptoms coincided with withdrawal of external B supply during the secondary growth of roots which involves the development of the primary cambium and secondary cambium arid leads to rapid root enlargement. Similarly, wheat sterility appears to involve B deficiency for periods as short as 5-7 days during critical stages of pollen development (Rawson, 1 996a).

Soil water. Dry soil decreases availability of many nutrients, primarily those nutrients which have low phloem (Mn, Ca, B) or low soil mobility (P, Cu, Mn). Many reports have noted that the onset of B deficiency in crops was associated with hot dry weather (e.g. Baker and Mortenson, 1966). While these observations are apparently explained by the fact that low soil water depresses B uptake (Hobbs and Bertramson, 1949), the effects of low soil water on B response are complicated by when the dry period occurs (Huang et al., 1997), and whether or not rainfall alleviates the period of drought. Detailed field studies by Noppakoonwong et al. (1997) on the response of black gram to B were the first to explore the implications of a period of low soil water for the diagnosis and prognosis of B deficiency. Adequate rainfall maintained soil water until day 40, after which a 25 day period of minimal rainfall caused soil water to decline progressively. During this period of drying soils, leaf B concentrations declined and induced severe B deficiency symptoms, particularly pod abortion except at the highest level of fertiliser B supply (Table 2). By plotting leaf B concentration at the end of the period of low soil water against pod number per plant. Noppakoonwong et al. (1997) were able to show that the critical concentration for diagnosis of B deficiency was not changed by the period of low soil water. That is pod set was related to leaf B concentration, which in turn was affected by soil water. However, the relationships between leaf B and seed yield for the prognosis of 13 deficiency varied depending on whether the leaves were sampled before, during or after the period of low soil water (Noppakoonwong, 1991). In that.

TABLE 2. Relationship between leaf boron (B) concentrations in black gram and soil water levels at three occasions during the growing season in northern Thailand. Values are means of four replicates ± SE for four levels of soil B treatment (kg borax ha^{-1}). From Noppakoonwong et al. (1997).

Days after sowing	Leaf B concentration (mg kg^{-1})				Soil water content (% w w^{-1})
	B0	B1	B4	B8	
40-42	11.8±4	22.3±3	28.7±6	46.6±2	15 ±1.5
58	8.6±3	11.7±3	13.4±2	21.3±1	10.4±0.4
90-92	12.6±3	14.5±2	20.5±3	29.3±5	15.8±0.9

particular field experiment, rainfall occurred during the mid-pod setting period so that as B uptake increased with increasing soil water content, pod setting resumed and largely compensated for the loss of pods that occurred during the dry period. Critical B concentrations for prognosis in that season declined from about 30 mg B kg^{-1} before flowering to 9 mg kg^{-1} during the period of drought (Table 3). The low critical concentration of 9 mg B kg^{-1} at day 70 seems anomalous, since it fell below the previously established critical concentration for diagnosis of B deficiency (12-18 mg B kg^{-1}. All the critical values for earlier sampling were equivalent to or greater than critical concentrations for diagnosis. By contrast, Rerkasem (unpublished data) reported for irrigated black gram grown on similar soils in the same environment that the critical B concentration in YFEL for the prognosis of B deficiency declined from about 45 mg kg^{-1} before flowering to 20 mg kg^{-1} during late pod setting. At equivalent growth stages, the critical concentrations were depressed in the rainfed situation (Table 3). In both cases, critical concentrations declined with time reflecting the decline in soil B supply. However, the differences between the two sets of results only serves to illustrate that a critical value for prognosis is a prediction of the possibility of a deficiency occurring for yield. In the rainfed environment, different patterns of rainfall particularly those that caused temporary *early* or terminal drought would have induced B deficiency at different stages of crop development and hence possibly produced different critical concentrations.

Better definition of the effect of low soil water on 13 response is needed. However, prediction of the risks of B deficiency in these cases may also be improved by measuring environmental data. For example, Lambert et al. (1997) have reported that prediction of 13 deficiency in pine trees *(Pinus radiata)* can be improved when rainfall, and age of trees are considered together with leaf B concentration. In plantation pines, rainfall is used as an indicator of seasonal droughts which depress B uptake, the consequence of which varies with tree age. Similarly, Ye et al. (1999) found that soil B levels alone were a poor predictor of

TABLE 3. Critical boron concentrations for prognosis of B deficiency for seed yield of black gram in an irrigated crop and in a rainfed crop subject to mid-season drought.

Growth stage	Irrigated crop[A]	Rainfed crop[B]
pre-flowering	30	31±3
first pod	25	30±4
first full pod	20	15±1
first mature pod	-	9±1

A. Rerkasem unpublished data
B. Noppakoonwong et al. (1997)

oilseed rape seedling mortality after transplanting in the field in southeast China in the late autumn. However, the prediction of seedling mortality in oilseed rape after transplanting was better predicted when rainfall in the month preceding transplanting was considered along with soil B levels since mortality varied markedly from year to year on the same soil depending apparently on the interaction of low soil B with low soil water.

The results above for plant response to B at low soil water all support the notion that B was phloem immobile and that B reserves in the plant at the onset of dry soil conditions were not remobilised to sustain plant growth once B uptake was impaired. However, recent research has shown that the phloem mobility of B is species dependent (Brown and Hu, 1996). Thus in those species which freely retranslocate B in their phloem, periods of low soil water are less likely to impair crop growth via B deficiency.

Low Vapour Pressure Deficit. Low vapour pressure deficits have been implicated for a long time in Ca-related disorders of vegetables such as lettuce *(Lactuca saliva)* and tomato *(Lycopersicum esculenlum)* (Grange and Hand, 1987). Such conditions often occur in vegetables grown in semi-protected or glasshouse environments but are not commonly experienced in field- grown vegetables. Recent evidence from studies on wheat in sub-tropical environments suggests that periods of low vapour deficit may be causally related to the lack of grain set in ears, known as sterility (Rawson, 1996b). Since the phenomenon of sterility induced by low VPD was identical to that induced by a short term withdrawal of external B supply (Rawson et al., 1996; Rawson and Noppakoonwong, 1996), Rawson (1996b) hypothesised that low VPD restricted the uptake of B into the ear leading to a deficiency of B for pollen development. Pollen sterility resulted in lack of fertilisation of florets in the ear producing sterility in wheat. The period when an ear was sensitive to withdrawal of B supply was about one week and coincided with the emergence of the flag leaf, that is before the ear emerges (Rawson, 1996a). Thus relatively short periods of low VPD, such as several days of foggy conditions that occur in winter in northern Bangladesh

are a plausible explanation for wheat sterility which can have devastating effects on wheat yield in farmers' fields. However, it is the variability of wheat sterility from year-to-year and spatially in an environment that makes it difficult to diagnose or predict by plant analysis. Rawson (1996b) suggests that the risk of wheat sterility can be predicted from pan evaporation values. At pan evaporation rates> 2.5 mm per day, B uptake by wheat in sub-tropical Asian environments was generally sufficient to prevent sterility except when soil B was very low; by contrast at < 1,5 mm daily pan evaporation during critical stages of pollen development, sterility risk was high especially at high temperatures.

CONCLUSIONS

Plant analysis is a powerful tool for diagnosing and predicting nutrient deficiencies in crops. However, in order to improve plant analysis as a methodology for crop nutrient management it is important to understand the reasons why it fails in some circumstances. Temporary nutrient deficiencies, discussed in the present paper are one of the significant causes of failure by plant analysis. Environmental factors which increase functional nutrient requirements have the potential to induce temporary nutrient deficiency but these interactions are not well enough understood at present. Low nutrient concentrations in planting seeds and in transplanted seedlings are also causes of temporary nutrient deficiency. Whilst such deficiencies can be diagnosed by plant analysis, very few critical concentrations have been developed for this purpose. Finally environmental factors like low soil water and low VPD which depress nutrient uptake are difficult to diagnose or predict by traditional plant analysis because of their difficult- to-predict temporal change. Progress in predicting these disorders will probably be made by combining plant analysis with the measurement of relevant environmental parameters.

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