Sterility in Wheat in Subtropical Asia: extent, causes and solutions

Proceedings of a workshop 18–21 September 1995
Lumle Agricultural Research Centre, Pokhara, Nepal

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Foreword: Purpose of the Project and Approaches

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WHEAT is a potential minor crop in warm subtropical areas of Asia, particularly in rotations with rice. Unfortunately, consistently high yields have not been achieved. One reason for this is the occurrence of sterility—the failure of grain-set in crops that have otherwise made adequate vegetative growth.

In the 1980s, researchers in Thailand, Bangladesh, China and Nepal began independently to work on the emerging problem of wheat sterility. Initial efforts to understand this problem centred on boron (B) because deficiencies of this micronutrient were known to induce sterility in other crops. In 1992, with support from the Australian Inter-national Development Assistance Bureau, scient-ists of the International Maize and Wheat Improvement Centre (CIMMYT) in Thailand, Chiang Mai University in Thailand and Murdoch University in Western Australia began working with Nepalese and Chinese scientists to investigate the response of wheat sterility to boron fertiliser, and to assess the variation that exists among cultivars of wheat in their ability to avoid sterility. Their results confirmed sterility induced by boron deficiency at some sites, but at others the causes were more complex. Meanwhile, researchers in Australia, notably at the CSIRO Division of Plant Industry in Canberra, had been investigating environmental factors affecting sterility in wheat, and concluded that many apparently conflicting results of temperature effects on sterility could be related to low vapour pressure deficits. Coincidentally, low vapour pressure deficits might also inhibit boron supply to the reproductive parts of wheat.

Drawing together researchers from the various groups that had worked on different aspects of the problem, ACIAR supported a 12-month study into the causes of wheat sterility.

The study had three components. Firstly, a workshop was held in Chiang Mai from 25 to 30 July 1994. The participants aired their views on what they knew or guessed were the primary causes of sterility in their regions. The workshop attempted to identify common threads and formulate experiments that could be done over the following year to test the ideas proposed. Secondly, the proposed experiments were conducted. Finally, another workshop was held at the Lumle Agricultural Research Centre, Pokhara, Nepal, from 18 to 21 September 1995. Results of the experiments were discussed in the hope of reaching some understanding of the problem and proposing solutions. The proceedings of the first workshop appeared as an Environmental Science Report of Murdoch University (94/6, July 1995), 'Causes of sterility in wheat', edited by R. W. Bell and B. Rerkasem. The contents of these Proceedings are drawn largely from the final workshop.

At the first workshop, the delegates differed in their ranking of the main determinants of sterility. Thailand and China ranked boron limitation first, but Nepal identified low temperature as being at least as important. Bangladesh considered high humidity and low light as the main determinants. Secondary factors which delegates guessed at as being important included high temperature (Thailand, Pakistan, China), waterlogging (all groups) and water stress (Thailand, Pakistan, Bangladesh).

The problem was to design experiments that would test the role of all these factors. It was decided to have a common field study in all participating Asian countries. The treatments were soil boron (2), genotype (3 or 4) and environment (3). The boron treatments were nil or 1 kg B/ha as borax; the genotypes were Fang 60 and SW-41 (previously shown by the Thai group to be tolerant and sensitive, respectively, to limiting soil boron) plus any local choices; and environment was varied by planting date. With six sites and three planting

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dates, there was a high chance of having several combinations of environment that would generate sterility and others that would not. The second planting date at each site was chosen as being likely to be most favourable for minimal sterility. The other two were selected as marginally too early and marginally too late for the region. A primary requirement of these studies was that the environment should be well described, and so meteorological instruments measuring temperature, humidity and light were provided by ACIAR to supplement readings from each group's local meteorological stations. These field studies formed the core of the research program.

There were also other controlled experiments to test specific hypotheses. These included a study in sand culture using pots located outside at Chiang Mai University. In this experiment there were three planting dates, as in the field studies, but boron and water applications were carefully controlled, thus avoiding any soil variables that might occur in a field study. This study assessed the effect on sterility of changes in the aerial environment associated with planting date. The study used a much wider range of genotypes than the field experiments.

Another series of studies was conducted at Murdoch University in Western Australia to examine whether a simple external plant measure, such as leaf elongation rate, might be used as a predictive indicator of impending sterility induced by low boron. (The more complex measure of potassium leakage was also tested.) The studies concentrated on the interactions between low temperature and low boron, which might give some answers to the problem in Nepal.

The final set of controlled environment studies was conducted in the CERES phytotron, Canberra, in eastern Australia. These studies attempted to assess the effects on sterility of the perceived key environ-mental variables and to examine the interactions between them. The initial workshop had provisionally identified the developmental stage of pollen meiosis to anthesis as being the period when most damage leading to sterility can occur. Therefore the Canberra studies exposed wheat plants to the combinations of environments only during that period. The variables chosen were humidity (high and moderate), light (moderate and low), temperature (high and moderate) and boron (low, limiting and adequate) in the two genotypes used in the common field studies, one tolerant of and the other sensitive to low boron supply.

These Proceedings present the findings of these studies. Most papers are in the form normally used in scientific journals, with an abstract, introduction, methods, results and discussion. This format leads to some repetition, but interestingly shows that, although there are trends in the data sets, there is still a range of opinion about what causes sterility in wheat in the subtropics of Asia. There are also several review papers and several ideas papers.

ACIAR wishes to express its appreciation to the participants in the project, and for their efforts in bringing together their findings for these Proceedings.

Review papers

A General Survey of the Incidence of Wheat Sterility

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Abstract

Sterility in wheat has been observed almost exclusively between 30°N and 30°S latitude. Its first large-scale sign is that florets remained open ('gaping glumes') for longer than normal at anthesis, giving ears a transparent appearance when viewed against the light. Anthers and pollen appear poorly developed and shrivelled. Such sterility generally results in reduced grain set and lower grain yield. Many factors have been linked to sterility, including boron deficiency, low temperature during reproductive development, waterlogging at flowering, low soil nitrogen and hot dry winds, but the link with boron deficiency is the only one that has been conclusively proved. In all areas where sterility has occurred, genotypes have varied in the degree of damage.

WHEAT sterility was first observed in Brazil in 1962 (da Silva and da Andrade 1980). Widespread sterility was observed in Nepal in 1964 when improved, high-yielding Mexican wheat was introduced, and in introduced Indian cultivars in the following year (Misra et al. 1992). Li et al. (1978) published the first report of large-scale sterility in wheat in the field. The report describes 40 000 ha of wheat in Heilongjiang Province in the north of China that set grain only poorly (giving grain yields of < 700 kg/ha) or not at all in 1972 and 1973.

The first symptom of sterility can be seen at anthesis. Florets remain open ('gaping glumes') for longer than normal at anthesis, giving ears a transparent appearance when viewed with the sun behind them (Li et al. 1978; da Silva and da Andrade 1983; Sthapit 1988; Rerkasem et al. 1989). When such florets are examined during anthesis, the anthers and pollen appear poorly developed and shrivelled (Li et al. 1978; Rerkasem et al. 1989). Da Silva and da Andrade (1983) associated sterility with the abnormal development of the male reproductive organs and called the problem 'chochamento', Portuguese for male sterility. In all the cited cases, sterility at anthesis resulted in lower grain yield or lower grain set.

Definitions of 'sterility', 'fertility' and 'grain set' in wheat differ somewhat among researchers and authors. Some of these are summarised in Table 1.

Incidence of Wheat Sterility

Geographical distribution

So far the report from Heilongjiang Province (latitude > 40°N) has been the only report of sterility in wheat outside the subtropics, although sterility in barley has long been known in Finland (latitude > 60°N) (Simojoki 1972). All other reports of sterility in field-grown wheat or with data indicating sterility have come from the tropics or subtropics (between the 30° latitudes) (Table 2).

Varietal susceptibility

Reports from several countries are summarised below. The most notable feature of observations of wheat sterility in most reports studied was the high degree of genetic variation found. The summaries include a preliminary assessment of genotype susceptibility to sterility based on available data. Susceptibilities are classified as:

- most susceptible—when the genotype has been reported with > 50% sterility
- moderately susceptible—when the genotype has been reported with 25% to 50% sterility
- least susceptible—when the genotype has never been reported with > 25% sterility, apart from under exceptional circumstances, such as in sand culture with no boron added.

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Table 1. Summary of some definitions of 'sterility', 'fertility' and 'grain set' in wheat, and other related measures

Publication	Term used	Measure
Single 1964	fertility, grain set	grains per ear
Li et al. 1978	sterile ear	no grain in any floret
	partially sterile ear	any grain set in up to half of florets
	fertile ear	all florets filled
Morgan 1980	% fertile florets	% florets with seed
Saini and Aspinall 1981	% grain set	% florets with grain (those florets judged potentially fertile)
da Silva and da Andrade 1983	% chochamento (% male sterility)	% florets without grain
Sthapit 1988 and Rerkasem et al. 1989	basal floret fertility (grains/F1+F2)	average number of grains in two basal florets of 10 central spikelets
Sthapit and Subedi 1990	% sterility	% florets without grain
Misra et al. 1992	% sterility	average sterility of 100 to 250 spikes felt by hand during grain filling, each graded as 100%, 75%, 50%, 25% or 0% sterile, by degree of absence of grain
	sterility	% florets with grain
Tandon and Naqvi 1992	% sterility	visual rating of gaping glumes at anthesis
Rerkasem and Loneragan 1994	grain set index (%)	% grain bearing in two basal florets of 10 central spikelets
Other related measures		
Beech and Norman (1966)	grains per fertile spikelet	
Midmore (1976)	number of grains per central spikelet	average number of grains in centre of ears large enough to have perfect floret

Nepal

A recent review by Misra et al. (1992) noted that sterility in wheat was first reported in the eastern part of the Nepalese Terai. Since then severe sterility has been seen often in other parts of the country. Factors suggested as responsible for sterility include boron deficiency, low temperature during reproductive development (Subedi 1992), waterlogging at flowering, low soil nitrogen and hot dry wind (Misra et al. 1992). Of all these factors, boron deficiency is the only cause that has been conclusively proved: sterility was effectively reduced by boron application (Sthapit 1988). In some cases, however, notably at higher altitudes, low temperature stress was suspected because boron application did not cure sterility (Sthapit 1988). Where sterility (measured as percentage of florets without grains) decreased with increasing levels of nitrogen fertilizer (Misra et al. 1992), it is not clear whether nitrogen increased the percentage of florets with grain through its effect on grain filling (source or photosynthetic capacity) or grain set (sink capacity through success of fertilisation).

Examples of genotypic variations in the susceptibility to sterility reported in Nepal (data from Sthapit et al. 1989):

- most susceptible: RR21 (= Sonalika), BL1022
- moderately susceptible: UP262, NL297
- least susceptible: NL460, Triveni.

Table 2. **Locations of sterility reported in field-grown barley (one report) and wheat**

Location	Latitude	Reference
Finland*	> 60°N	Simojoki 1972
China: Heilongjiang	> 40°N	Li et al. 1978
China: Yunnan	20°–25°N	Yang 1992
Bangladesh	23°–27°N	Rerkasem, Saunders and Saifuzzaman, unpublished
Brazil: Minas Gerais, São Paulo	19°–23°S	da Silva and da Andrade 1980
Nepal	27°–30°N	Sthapit 1988; Misra et al. 1993
India: West Bengal, Assam, Orissa, Bihar, along India–Nepal border	20°–27°N	Tandon and Naqvi 1992
Thailand: Northern region	19°N	Rerkasem et al. 1989
Australia†: Ord River	16°S	Beech and Norman 1966
Mexico†: Poza Rica	20°N	Midmore 1976
Uganda‡	0°	D. A. Saunders (pers. comm.); D. J. Davidson (pers. comm.)

* Barley

† These two reports were not concerned with sterility, but their data indicated some severe sterility (see 'Other countries' section).

‡ Diagnosed as boron deficiency.

Bangladesh

Published reports about wheat sterility in Bangladesh are few. However, those of us who have visited the country's wheat fields during anthesis (March–April) have seen more gaping and transparent ears than in any other wheat-growing country. Some recorded observations exist; for example, the following from D. A. Saunders (pers. comm. 9 October 1989):

'In 1986/1987, massive sterility was observed in the northern wheat zone of Bangladesh. In that year, yield losses due to sterility were predominantly in the variety Kanchan. Sonalika was little affected. Farmers naturally thought it was a varietal problem.

'Soil analyses indicated low boron levels in the areas affected by sterility.

'In 1987/88, a series of unreplicated test plots were placed in farmers fields. Results were received from 29 sites indicating a mean response to boron application of 14% with Sonalika slightly more affected than Kanchan. In 1988/89, results from 43 tests showed a mean yield response of 12.1% from Kanchan and 8.5% for Sonalika.

'These data indicate that substantial yield response (equivalent of approximately 60% of the yield gains due to plant breeding in the last 20 years) may result from boron application in Bangladesh, and also demonstrate the complexity of the environmental interaction (year to year).'

Reuter (1987) also noted severe sterility in some wheat genotypes in Bangladesh.

Brazil

Wheat sterility was first observed in 1962 in irrigated varzeas (flood plains) of São Paulo and Minas Gerais (da Silva and da Andrade 1980). A similar problem was later observed on the virgin red-yellow latosol of the Cerrados in a three-year experiment conducted from 1979 to 1982 (da Silva and da Andrade 1983). In both cases boron application significantly increased grain set and grain yield.

Examples of genotypic variations in the susceptibility to sterility reported in Brazil (data from da Silva and da Andrade 1980):

- most susceptible: Confianca, Medias, IAS 55, IAC 5, Zaragoza
- moderately susceptible: Medias Gerais, Londrina, Sonora 63
- least susceptible: Jupateco.

India

Widespread wheat sterility in the state of West Bengal has been attributed to boron deficiency (Reuter 1987). Janak, UP262, BW43, BW5 and

BW11 were among genotypes noted for susceptibility. Several published papers from India have reported sterility in wheat caused by boron deficiency (e.g. Ganguly 1979; Mandal and Das 1988). According to Tandon and Naqvi (1992), widespread sterility can be found in West Bengal, Assam, Orissa and along the Indo-Nepal border.

China

Mann (unpublished report), visiting Dehong Prefecture in Yunnan Province (latitude about 24°N) in 1990, reported:

'Major problems: Empty heads, premature leaf senescence, and leaf rust on the increase. Empty heads are promoted by sandy soil, late sowing, and low P. It is reduced under trees, through early sowing, P fertilizer, more irrigation and B fertilizer.'

'In one village, fields showed variable degrees of sterility most probably due to boron deficiency. Boron fertilization did not always solve the problem completely.'

I visited Yunnan with Mann in March 1992 and found 'sterility'—that is, transparent wheat ears with gaping glumes at anthesis—to be common in Dehong Prefecture. I also saw the symptom at Yuxi, close to Kunming. Mrs Yang Yanhua of the Yunnan Academy of Agricultural Science reported that sterility is common in Dehong, Baoshan, Simao and Xishuangbanna. At Luxi (a county in Dehong Prefecture) we saw quite a few hectares of Spring 980 (Ald/Pci) that were almost completely sterile. Yield loss was estimated at about 90% by the director of Luxi County Agricultural Research Institute. Local wheat workers reported anecdotes of severe sterility in previous years:

- In Ruili, a county on the Burmese border, 40% to 50% yield loss with the variety Spring 980 in one area of 230 ha in 1984.
- Total loss of 40 ha of variety 0103, but 0.2 ha of Sonora 64 was unaffected.
- 3 ha of Spring 980 in Ying Jiang county that was completely sterile (see also Yang 1992).

During our 1992 visit, we also recorded sterility in some late planted De Mai 3, which had a grain set index of 74% to 78%. At a site in Ruili with a high water table, Mian Yang 11, a variety noted for not being susceptible to sterility, had a grain set index of 68% to 78% compared with 91% where it was not affected by waterlogging. At Yuxi near Kunming, gaping glumes were also observed in a potential yield trial of 0103 and a reselection from it, called 87-1.

Thailand

The total planted area of wheat in Thailand is very small. Sterility has been seen every year in screenings and yield trials at Chiang Mai and Samoeng (e.g., see Rerkasem et al. 1989 and Rerkasem 1993). I have seen sterility in Inia 66 in farmers' fields. SW-41 (BAYA/EMU), now used as the sterility sensitive check, was sterile in the Thailand Yield Nursery of 1986–87. Many otherwise promising genotypes have been eliminated because of their susceptibility to sterility. This might explain why many wheat cultivars released in Thailand have included some 'very old' varieties such as Sonora 64 and 1015 (PI/FD//PI/MZ/3/MXP, which was bred in Pakistan in 1977 and named Bulbul, and released in Thailand as Fang 60 in the 1980s). These last two are also least susceptible to sterility. Promising lines from onstation selections have also been found to be sensitive to sterility once they were tested onfarm; for example, ARTC 87001 (Junco 'S'/Buc 'S', CM64478, from the 4th Hot Climate Wheat Screening Nursery) (Rerkasem 1993) and SMGBW 88001.

Other countries

In the early 1960s a series of experiments tested wheat and other species for their potential as irrigated dry season crops at the Kimberley Research Station in the Ord River Valley of Western Australia, at latitude 15°7′ S (Beech and Norman 1966). All four wheat cultivars tested set about 2 grains per fertile spikelet when sown April 24 or May 30. The number of grains per fertile spikelet in all four cultivars declined with delayed sowing date. When sown on 6 August, Wit Spitkop, a South African cultivar, set virtually no grain, and two standard Australian cultivars, Gamenya and Gabo, had only 0.4 to 0.7 grains per fertile spikelet. D. F. Beech (pers. comm.) has recently reported a response to boron in wheat in the Kimberley region. Midmore (1976) conducted studies in Mexico in the 1973–74 and 1974–75 growing seasons and reported grain-set data that reflected severe sterility at Poza Rica (latitude 20°29′ N). For example, genotypes such as Era, Mexico 120, Tcl.v.404, Tcl.PM312, Meng.8156, Yecora, Anza (WW 15) and Kloka recorded grain set (in grains per central spikelet) equivalent to a grain set index of only 8% to 49%. Recently a report came from Uganda (from D. J. Davidson, an agronomist working on a wheat development project in Uganda) of widespread boron deficiency at all the project's working sites.

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Parameters Likely to be Associated with Sterility

H. M. Rawson*

Abstract

This paper proposes a definition of plant sterility, examines how several components of the environment might induce it, and discusses what stages in the plant's development might be most sensitive to the environmental perturbations that lead to sterility. It suggests how the seemingly complex and interactive effects of the weather on sterility might be operating largely through one avenue in the plant, namely, the movement of essential micronutrients from the soil to the generative zones of the plant at around the stage of pollen meiosis. It discusses the relationships between temperature, humidity and radiation in so far as they drive growth rate, and, by corollary, the duration of the critical growth stages, and how they interact to control movement of water and micronutrients into the plant.

Definition of Sterility

Before we can come to any consensus about the effects of the environment on sterility, we have to agree on the characteristics of a fully fertile plant. In its broadest sense, a sterile floret is one that has no grain at plant maturity. Using this definition, however, even the most perfect wheat heads are partially sterile because of the sequential nature of development. In every head, the last one or two florets to be produced in each spikelet do not develop far enough or grow large enough to have floral parts before the earliest florets in the spikelet are already filling grain (e.g. Rawson and Bagga 1979). So within this definition, a perfect 20-spikelet head with 50 grains must have at least 25% sterile florets. This definition is not useful for our requirements. We need a definition that discounts such 'normal' sterility. The system used by Rawson and Bagga (1979) assumed that in all spikelets, any terminal florets with lemmas less than approximately 3 mm long should be discounted from any sterility index (and see fertility maps of Rawson 1986a based on this concept). All florets proximal to those and with longer lemmas should be potentially fertile unless the material used had genetic basal sterility (Frankel et al. 1969). Within that definition, which will be used here, ears can be fully fertile.

The sequential and asynchronous nature of ear development

Development of the ear can be seen microscopically from when double ridges are laid down on the growing apex (e.g. Bonnett 1935). Each double ridge is made up of a lower leaf primordium ridge and an upper branch primordium, which eventually becomes the spikelet. Even at that stage the sequential nature of development can be seen at the apex. The spikelets that become the lower central part of the ear appear as double ridges first. Development proceeds laterally and longitudinally from that point until eventually the basal spikelet above the collar differentiates and the terminal spikelet appears. Depending on whether conditions are correct to satisfy the flowering requirements of the genotype (long days, completion of vernalisation, high radiation), the central spikelets could already have floret primordia before the terminal spikelet has appeared (Rawson 1971). In extreme situations, the terminal might never form (Manupeerapan et al. 1992). This lack of synchrony in different parts of the ear continues so that anther initials can be developing in floret 1 of spikelet 4 from the base of the ear at the same time as glume initials are appearing in floret 2 of spikelet 15 (and see micrographs in Moncur 1981).

Lack of synchrony in development and the mapping of sterility

Lack of synchrony has its benefits for both the plant and our analysis of sterility. For the plant, it

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means that brief stresses might damage only those florets that are passing through a sensitive phase during the stress; others will survive. For our analysis, it means that we can pinpoint the timing of the stress by mapping the distribution of sterility within the ear. If whole ears are sterile, we can conclude that the stress was lengthy (6 to 10 days, see later), or of such severity that it killed all developing plant tissues (–4°C frost), or that there was a general nutritional disorder that affected a sensitive stage whenever the stage occurred. We can almost definitely conclude the latter if all ears are sterile, particularly if the genotype is one in which tillering is asynchronous.

Abnormal floral development in the subtropics (developmental sterility)

Most wheats have been developed for temperate regions and almost invariably flower during increasing day length. Many flower earlier after they have been exposed to a period of cold (e.g. review by Slafer and Rawson 1994). If genotypes that have moderate to significant responses to photoperiod, cold or both are grown in warm climes and under low radiation, floral development can be upset. In subtropical Asia, with its warm conditions, periods of low radiation, and close to 12-hour day length (11.1–12.9 h at 15°N; 10.8–13.2 h @ 20°N), it is more likely that developmental sterility will occur under these conditions than in the traditional wheat zones (Rawson and Richards 1993; Rawson and Zajac 1993). Indeed, under these warm conditions, the phasic stages of ear development can be significantly delayed (Rawson 1993a, b). Although delay in temperate regions is usually associated with greater production because more floral parts are developing during the delay, in subtropical conditions it can result in floret infertility because low source to sink ratios reduce or stop the production of new parts and prevent the completion of development of others.

To avoid such developmental sterility, it is advisable to avoid genotypes with any response to vernalisation if it is likely that low radiation will coincide with high temperature during the developmental stages leading up to terminal spikelet formation (Midmore et al. 1982). If it is necessary to extend the vegetative stages, it would be advisable to extend the basal vegetative phase (Vongburi 1992), though making allowance for the different sensitivities among genotypes of this phase to temperature (Slafer and Rawson 1995a).

Mechanical sterilisation and compensation

It is worth noting that some of the older wheat genotypes, before Norin 10, are conservative in grain set, so they can have relatively large distal florets that are empty. These large florets are not necessarily irreversibly sterile. When lower florets in the same spikelet are mechanically sterilised, they can then become fertile (Rawson and Evans 1970; Bremner and Rawson 1978). It seems that competition for assimilates within each spikelet can be quite intense during the period immediately after anthesis, and the earliest florets to be fertilised (the basal ones, which are developmentally most advanced) are at an advantage. Hence, the upper florets, which may be delayed by three to four days because of the sequential nature of development, do not necessarily complete their floral development. This can provide the plant with some potential for compensation if the basal florets are sterilised by a brief environmental event. It is important when deciding on a sterility index to allow for such characteristics of these older genotypes.

Most Sensitive Phases for Sterility Caused by Environment

Pre-heading and the minimal effect of carbon availability

It is generally considered that the period when floret numbers are most sensitive to environmental fluctuations is during the two to three weeks before heading through to anthesis. This is the time when new florets are being added and others are developing. Any change in carbon availability at this time also changes the numbers of fertile florets produced. Thus, increases in radiation and carbon dioxide or reductions in temperature during this period increase grain numbers per unit ground area (Fischer 1985b; Fischer and Aguilar 1976; Wardlaw 1994). This occurs through an increase in numbers of florets, not by any increase in percentage floret fertility. Conversely, reductions in carbon availability during this time curtail the developmental process resulting in fewer florets and, similarly, probably have minimal effects on percentage floret fertility.

Emergence of the flag leaf ligule and meiosis: a critical phase

Though carbon availability at this time is unlikely to affect fertility, it is during this phase that other variables can have the greatest effect on fertility, particularly by damaging the process of pollen meiosis and meiosis in the megaspore mother cell (see Bennett, Finch et al. 1973 and Bennett, Rao et al. 1973 for a description of the stages). Anther infertility then becomes most obvious a few days later at anthesis when the lodicules in the florets can remain swollen for several days, keeping the florets gaping wide to receive external pollen.

Pollen meiosis is spread over a few days, because of the pattern of development discussed above, but it does occur while the ear is in the boot before the ear starts to emerge. According to Dawson and Wardlaw (1989; see for staining method), the sensitive pollen mother cell stage occurs immed-iately after the ligule of the flag leaf can be seen, and before head emergence. It is important to establish that these associations of leaf and ear development are generally correct so that external features can be used as developmental markers.

It has been suggested that water stress at this critical time has its effect primarily on male sterility (Bingham 1966; Saini and Aspinall 1981, 1982b), and so fertility can be regained by cross-pollination, though the seed produced will be hybrid. By contrast, heat stress affects both female and male organs (Saini et al. 1983) and so is more serious. Saini and Aspinall (1982b) propose a link between high abscisic acid (ABA) concentrations and male sterility induced by water stress, but suggest there is no link between ABA and temperature effects.

It is important to note the conditions under which the Saini studies on heat stress were done, as they are relevant to the questions we are asking; we will discuss their effects later in this paper. Plants in growth cabinets were exposed to high temperatures (30°–40°C) for only 24 hours at pollen mother cell stage (as determined by squashed and stained pollen grains), relative humidity was maintained above 70% throughout (to prevent aerial water stress), and light levels were 350 μmol/m^2/s for 16 hours, approximately equivalent to 17% full sunlight or overcast conditions.

The whole period of heading to shortly after anthesis

Data from controlled environments with a range of genotypes (Dawson and Wardlaw 1989) suggest that the period immediately following head emergence is relatively insensitive to environmental perturbation. Dawson and Wardlaw's detailed studies of the effects of high temperature at this stage showed no significant reduction in grain number per spikelet.

Low carbon availability from just before to just after anthesis can produce failed or 'sterile' grains in distal florets, particularly towards the apex of the ear (Rawson and Ruwali 1972). It seems that these grains start growth but are then reabsorbed, reaching a dry weight of no more than 3 mg. These small grains caramelise to a dark brown colour when oven-dried. This stage of development seems to be far less sensitive to environmental sterilisation than the period of pollen meiosis, though Tashiro and Wardlaw (1990) did count up to 50% sterile grains resulting from high temperatures two days before anthesis.

Weather in the Subtropics and Differences from Temperate Zones

Environmental sterility appears to be a problem almost exclusively of the Asian subtropics. It is not regarded as being of significance in Australia, where maximum temperatures can also be high. This conclusion applies to areas such as Roma (central northern Queensland, Rosalind Jettner, pers. comm.) and the Toowoomba area in southern Queensland, except in small areas where copper is deficient (David Woodruff, pers. comm.), and in glasshouse studies. It has been recorded in the Ord River valley in northern Western Australia under irrigation, but this was some 25 years ago using very early Norin 10 material (Beech and Norman 1966).

Table 1, taken from Fischer (1985a), shows some of the key features of the weather in the tropics and subtropics. Generally, mean temperatures are high, with day/night amplitude increasing with distance from the equator and oceans, and with increasing elevation. Daily radiation is generally high. Relative humidity, however, differs considerably, ranging around 70% for most places apart from the arid continental zones of Australia, India and Africa. Actual vapour pressures largely

Table 1. Actual and possible wheat-growing locations in and near the tropics, and principal features of their temperature and humidity regimes in January in the northern hemisphere or July in the southern hemisphere (from Fischer 1985a). RH = relative humidity, VP = vapour pressure in millibars, VPD = vapour pressure deficit, also in millibars

Thermal and humidity regimes	Location	Lat.	Alt. (m)	Mean daily January or July weather						Total rain		Locations with approx. similar wheat climates
				Mean temp. (°C)	Temp. range (C°)	RH (%)	VP (mb)	VPD (mb)	Solar radn (MJ/m^2/d)	Dec.–Feb. (mm)	Ann. (mm)	
Very hot, humid	Los Bãnos, Philippines	14°N	40	24	5	80	24	6	15	230	2040	Jakarta, Indonesia
	Phitsanulok, Thailand	17°N	50	25	14	76	24	8	–	32	1354	
Very hot, dry	Khartoum, Sudan	16°N	380	24	16	27	8	22	20	0	164	
	Kununurra, Australia	17°S	30	23	17	32	9	19	21	5	745	
Hot, humid	Chiang Mai, Thailand	18°N	313	21	15	76	19	6	22	28	1246	Mandalay, Burma
	Dhaka, Bangladesh	24°N	8	19	14	73	16	6	15	51	1928	Poza Rica, Mexico
	Formosa, Brazil	16°S	911	19	14	64	14	8	–	17	1995	Villa Guede, Senegal Santa Cruz, Bolivia Asunción, Paraguay
Hot, dry	Kano, Nigeria	12°N	470	22	17	23	6	20	21	1	873	Hyderabad, India
	Indore, India	23°N	555	18	17	44	9	12	18	16	876	Taiz, Yemen Rep. Tlaltizapan, Mexico
Warm, humid (12°–25° lat.)	Lima, Peru	12°S	11	15	4	94	16	1	21	5	10	Lusaka, Zambia
	Emerald, Australia	23°S	179	15	16	70	12	5	–	108	591	Londrina, Brazil
	Harare, Zimbabwe	18°S	1470	14	15	56	9	7	18	9	868	Matamoros, Mexico
	Guangzhou, China	23°N	18	14	9	75	12	4	–	126	1720	
Warm, humid (25°–30° lat.)	Riyadh, Saudi Arabia	25°N	594	15	14	64	11	6	–	42	105	New Delhi, India
	Ciudad Obregon, Mex.	27°N	40	15	16	82	14	3	13	40	267	Kufra, Libya
	Passo Fundo, Brazil	28°S	750	13	–			–	–	445	–	Cairo, Egypt
Temperate	Canberra, Australia	35°S		6	14	60	8	5	10			

reflect this pattern. The relevance of vapour pressures (VP) and vapour pressure deficits (VPD) will be discussed later.

The main difference appropriate to the vegetative phase of wheat between weather conditions in the subtropics and in temperate zones is in temperature. I have used Canberra as an example of a temperate zone (because I had the data). Absolute temperature is much lower, but the range is similar to that in the tropics; relative humidity and VPD are also similar; but solar radiation is much lower because of the short day length of 9 h in winter. (See Fig. 1, relationships between latitude and photoperiod, and Fig. 2, relationships between photoperiod and daily radiation.)

Photoperiod and radiation

At the equator the photoperiod remains close to 12 hours throughout the year, but with distance from the equator the difference between the shortest and longest day increases. Figure 1 shows that for wheat-growing zones (0°–55° latitude), photoperiod can differ by up to 5 hours a day. Knowing the photoperiodic range is important for choice of a genotype with the appropriate photoperiodic sensitivity as flowering too early or too late could result in no yield.

Associated with day length is the amount of radiation received per day. This is shown in Figure 2, where radiation is linearly related to day length. In essence, this means that if there is no cloud, the amount of light available to plants for growth during the growing season increases considerably with latitude. So, providing that temperature is not a limitation, potential growth at these high latitudes is very high for short periods of the year. By contrast, in the tropics, potential growth is moderately high throughout the whole year.

Changes in weather during the season and correspondence of stages of development

The comparison in Table 1 between temperate and tropical zones is an oversimplification because it considers only one month of the year. In temperate zones, wheat can take nine months from seed to seed. Figure 3 shows changes in temperature, radiation and photoperiod for a typical wheat-growing area in southern New South Wales (Australia), taken from Lopez-Castaneda and Richards (1994). Points to note are that sowing occurs when temperature and photoperiod are

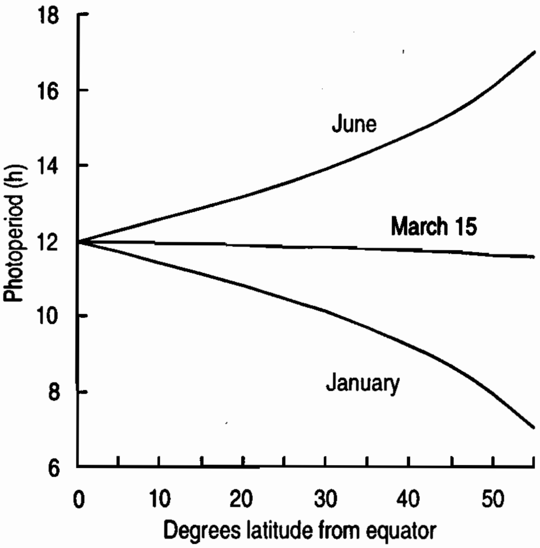

Figure 1. Change in photoperiod with distance from the equator for the wheat-growing regions of the world showing values for the months with longest and shortest photoperiods (June and January). The difference between these two values gives the range in photoperiod for any location

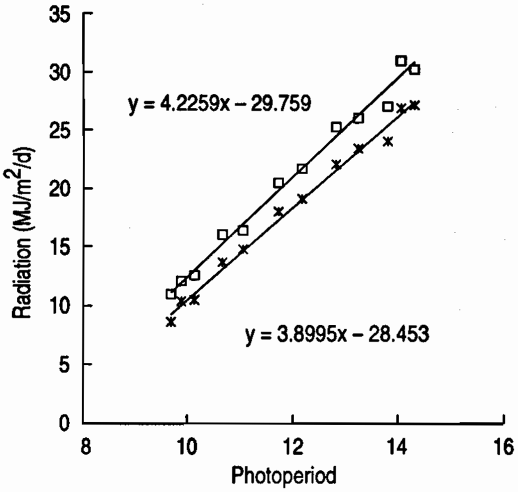

Figure 2. Dependence of monthly radiation on photoperiod. Data taken from Canberra (35°S), showing the average value for each month between 1976 and 1990 (lower line) or showing only the brightest month for the 14 years (upper line; that is, approaching potential radiation for the month)

declining to their minimum before they rise rapidly towards the heading and grain-filling periods. Thus plants achieve some growth before being exposed to the low temperatures and short photoperiods when vernalisation occurs leading to the double ridge stage. Figure 4, taken from Slafer and Rawson (1994), shows the stages of development of wheat in relation to the building of components of yield.

Hypothesis for Why Sterility Occurs in the Subtropics

I would like to suggest an hypothesis that might explain how differences in weather patterns between the subtropics and temperate zones might control the occurrence of sterility:

> Field sterility results primarily from limitations in particular trace nutrients at reproductive sites during meiosis. This can occur from various combinations of several factors such as low soil availability of the nutrient, low uptake rates into the roots, low transport rates through the xylem (associated with low transpiration) or through the phloem (low carbon levels because of low radiation), and the short period of development for the use of these nutrients, which is shortened further by high temperature.

Some questions on nutrition relating to the hypothesis

The trace nutrients could include copper and boron. The importance of boron is covered in other papers in these Proceedings. Questions that should be addressed in future research include:

- What are the relative effects of trace nutrients on general growth and fertility? Can symptoms be seen before real damage occurs?
- How much boron is needed by the plant at key stages? What concentrations are required in the soil and what uptake rates are required?
- What proportion of boron uptake from the soil is actively linked with transpiration rate? T. F. Neales (pers. comm.) suggests that it could be high.
- What is the relationship between boron concentration in the xylem and flux? Does concentration increase with reduced transpiration to equalise the amount in transit, or does the amount of boron moved through the plant depend primarily on transpiration rate? (See Munns (1985) for fluxes of other ions.)
- What transpiration rates are required at different concentrations of soil boron to avoid sterility, or is rate unimportant?
- As meiosis occurs before the ear emerges and before ear transpiration begins, does boron movement into the florets depend on building up high concentration gradients? Is movement by diffusion, as suggested in some old publications? If that is the case, is a high concentration gradient of sucrose needed to move the boron into florets (Rawson and Constable 1981)?
- If steep gradients of sucrose are required, does low radiation reduce boron movement through the association with low carbon fixation?

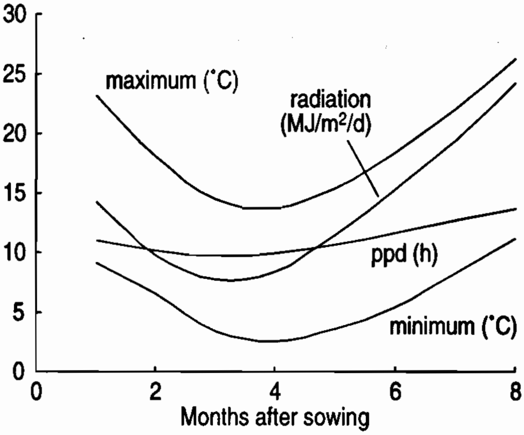

Figure 3. Temperature, radiation and photoperiod during the growth of wheat crops in southern New South Wales, Australia, and showing the range of timing of the double ridge phase (DR) among genotypes (from Lopez-Castaneda and Richards 1994)

Weather Effects on Sterility

Effects of high temperature on accelerating development rate

Temperature has its most obvious effect on plants in affecting their rate of development. Generally, as temperature rises, organs such as leaves, roots, tillers, spikelets and florets appear in progressively less calendar time; in annual crops, the life-cycle can be completed earlier. The effects of temperature on rate have been well described quantitatively through the concept of plant time or thermal time (Nuttonson 1948). In its simplest form, this

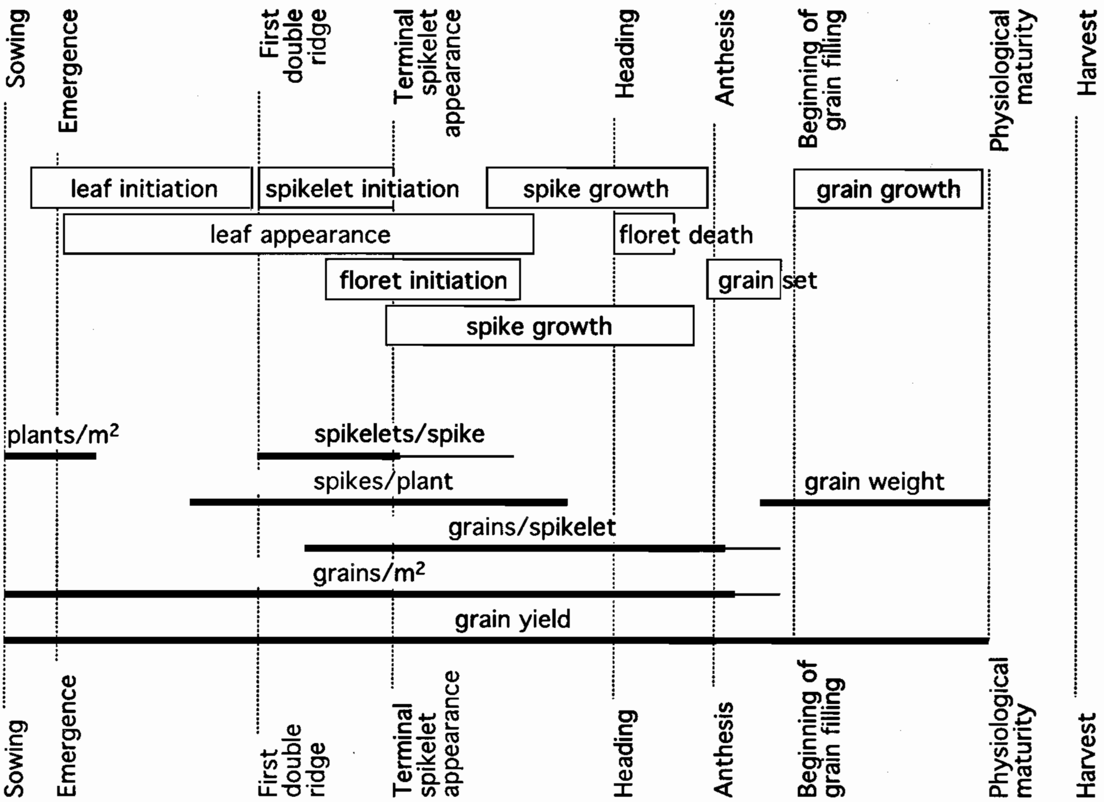

Figure 4. Stages of development in wheat (from Slafer and Rawson 1994)

is calculated by summing mean daily temperatures. Thus, a plant growing during a day with a mean temperature of 20°C will accumulate 20 degree days (°Cd) on that day. Calendar time will be one day but plant time will be 20°Cd. During five days at that temperature the plant will accumulate 100°Cd. The concept has to be used with some caution at high temperature because development does not respond linearly to temperature then (Rawson 1993b, Rawson and Richards 1993), and there is always considerable discussion of the appropriate base temperature to use (Slafer and Rawson 1995b).

The concept becomes very useful for calculating how long particular processes will take when the temperature is known. For example, a new leaf might appear on plants of a particular genotype every 80°Cd (that is, the plant's phyllochron interval). This is four days at 20°C or eight days at 10°C. Similarly, a spikelet might appear approximately every 10°Cd (Rawson 1987). The same type of relationship is likely to apply to processes such as floret development and meiosis. Thus although a particular developmental process might take a constant thermal time irrespective of temperature, it can take different numbers of days. This can create a problem for the plant if there are any growth processes that are not driven by temperature. For example, the shortening of a developmental process by increase in temperature will reduce the number of days during which radiation can be captured for use in growth. Therefore the organ involved will be smaller because less carbon will have been fixed during its development. Equally, there will be less time for nutrients to be absorbed and moved in the plant, so again this could result in the organ being smaller. In short, increases in temperature can have their greatest effect on the plant by making the resources for growth relatively more limiting (Rawson 1990).

This speeding of development might have its consequences for sterility. A shorter period for phases such as meiosis in environments where key resources such as boron are already limiting could make the difference between fertility and sterility by reducing the period during which boron can be available for that developmental process. To understand sterlility in wheat, we need to know how long the key processes take and how they are modified by temperature. For example, how many hours or days is a floret susceptible to male and female organ damage, how is that period changed by temperature, and how long does the process take for the whole ear?

For any calculations of thermal time for these processes, it seems likely from interpolating the data of Slafer and Rawson (1995b) that the base temperature (below which development ceases) will be about 7°C, though it should be remembered that base temperature seems to range over about 3° between genotypes. If we assume that the ear takes five days at 15°C to complete meiosis, this comes to 5 d × (15°C – 7°C) = 40°Cd. At 25°C this 40°Cd is equivalent to only 2.2 days (40°Cd / (25°C – 7°C) = 2.2 d). Therefore a very short period of environmental stress at this temperature could sterilise whole ears.

Direct effects of high temperature on sterility

The work of Saini and Aspinall (1982b) appears superficially to be the most relevant for considering direct effects of temperature on sterility. Their data show a dramatic reduction in grain set with increase in temperature above 20°C during pollen mother meiosis (Fig. 5). They carefully avoided any water stress during the study, keeping leaf water potential high throughout, and so concluded that the effects on sterility must be due only to temperature. However, the other conditions imposed were high humidity and low radiation. So according to my hypothesis, the treatment would not only accelerate development, but would minimise transpiration and uptake of inorganic compounds, and minimise fixation and concentration gradients of carbon. So the apparent temperature effects could have been effects on the availability of trace nutrients.

In a study of 24 wheat genotypes grown throughout their life-cycles at 30°C day and 25°C night temperatures, I found sterility in only five genotypes (Rawson 1986a), and in only one genotype (Olsen) at the serious levels of the Saini and Aspinall work. However, I grew my plants under high natural radiation through summer and at low humidity, so it is possible that the difference in fertility between the two studies (Rawson and Saini) was related to differences in humidity and radiation. It is also possible that high temperature on its own has no influence on sterility. Data from Dawson and Wardlaw (1989), collected in naturally lit glasshouses with uncontrolled humidity, suggest great variation in response among genotypes in response to high temperature (30° day / 25°C night) at emergence of the flag leaf ligule (Table 2). Dawson and Wardlaw included Gabo, the cultivar used by Saini and Aspinall (1982b), and found it to be only moderately sensitive to high temperature, having a reduction in grain set of only 24%. This again suggests that humidity and radiation levels could have been key factors in causing sterility in the Saini and Aspinall work. Interestingly, results of whether high temperature at the boot stage made pollen non-viable were very variable, but Dawson and Wardlaw (1989) did not explain why.

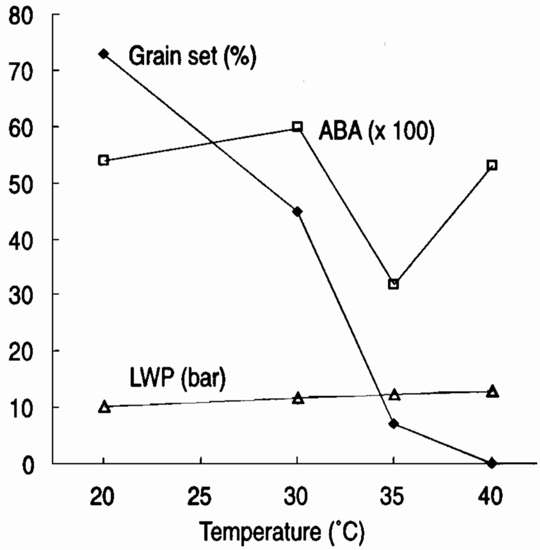

Figure 5. Increasing temperature during pollen meiosis reduces fertility in wheat. Humidity was maintained above 70% so that leaf water potential (LWP) did not decline. ABA (abscisic acid) content was unaffected by treatments (from Saini and Aspinall 1982b)

Some recent work on bean (*Phaseolus vulgaris* L.) grown at 22°/17°C examined sensitivity to high temperature at different stages of floral develop-

Table 2. Percentage reduction in kernel number with an increase in temperature from 18°/13°C to 30°/25°C during the booting stage. From Dawson and Wardlaw (1989)

Cultivar	% reduction due to high temperature
Brevor (USA)	88.3
Oligoculm 112-76 (Israel) (*n*= 2)	88.1
Svalof's Parl II (Sweden)	74.6
Centurk (USA)	67.2
Pinnacle (*n* = 3)	66.9
Olympic	63.4
H757 (Afghanistan) (*n* = 2)	60.3
Highbury (England)	54.7
Mendos	48.8
Dundee	48.5
Sonalika (India)	45.5
Zenati Boutielle (Mediterranean) —durum	44.8
Condor	42.8
Durati (durum)	41.9
Bencubbin (*n* = 2)	36.5
Songlen	35.0
Kalyansona (India) (*n*= 8)	31.7 ± 5.6
Kite	30.1
Banks (*n* = 9)	29.9 ± 4.3
Gabo (*n* = 2)	24.3
Florence Aurore 8193 (North Africa) (*n*= 3)	22.9
Norin 10 (Japan)	21.0
Lyallpur (Pakistan) (*n* = 2)	20.3
Heron	19.5
Trigo 2 (Philippines)	19.0
Timstein (USA)	17.6
Sun 9 E	11.1
Hybrid Titan	10.7
Trigo (Philippines)	9.6
Isis	7.4

ment (32°/27°C for 5 days) and concluded that sporogenesis is most susceptible (Gross and Kigel 1994). Table 3 presents these results. Figure 6 shows that seed set increased with lateness of high temperature after this stage. The authors used the same approach as Saini and Aspinall (1982b) of maintaining low VPD (8 mb in this case) during their high temperature treatments to minimise water stress. However, they used high light of 1200 to 1550 µmol/m²/s.

Genotypes are differentially sensitive to high temperature

Dawson and Wardlaw (1989) ranked a range of genotypes for response to high temperature (30°/25°C) during the booting stage. They found a reduction in grain set ranging from 7% to 88%; most genotypes fell in the 30% to 40% range. A Philippine line (Trigo 1) and a genotype from Pakistan (Lyallpur) were among resistant material. Interestingly, the Indian genotype Sonalika (RR 21 in Nepal), which according to Mandal (1991) has no response to boron, ranked only moderately (45% reduction). This suggests that Sonalika can become sterile from high temperature in the absence of any boron effect (and see complementary findings by Tiwari, these Proceedings).

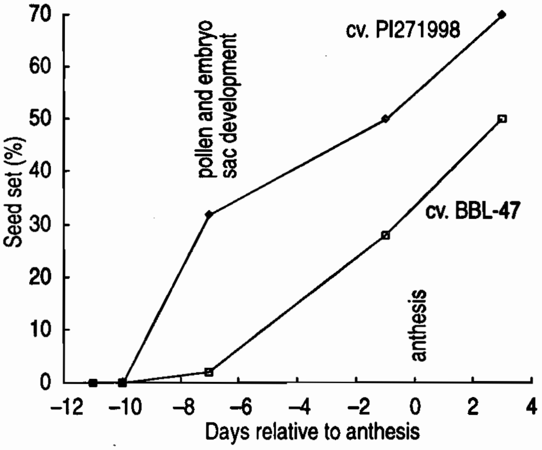

Figure 6. High temperature (32°/27°C for 5 days) causes the greatest reduction in fertility of bean plants at 12 to 10 days before anthesis (from Gross and Kigel 1994)

Table 3. Timetable of male and female development in bean (BBL-47 and PI-271998) plants grown at 22°/17°C. (Timings and stage of reproductive development after exposure to 32°/27°C are indicated for different experiments from Gross and Kigel (1994))

Reproductive stage	Days after sowing	Days rel. to anthesis	Timing and reproductive stage during exposure to 32°/27°C
Thin-walled microsporocytes Megasporocyte	20	(–12)	Micro- and macro-sporogenesis (Exp. 1)
Thick-walled microsporocyte	22	(–10)	
Tetrads Megaspores	24	(–8)	Pollen and embryo sac development (Exp. 2)
Free microspores	26	(–6)	
Visible endothecium Interlocular septa disintegrates	28	(–4)	
	30	(–2)	Anthesis and early pod development (Exp. 3)
Complete embryo sac Pollination Fertilisation Two-cell embryo	32	Anthesis	
	34	(+2)	One-day-old pod (Exp. 3)
Globular embryo	36	(+4)	Three-day-old pod (Exp. 3)
	38	(+6)	
	40	(+8)	

Temperature affects transpiration rate via VPD, and how this might affect sterility

As temperature rises, the capacity of the air to hold water vapour rises (Fig. 7). For example, when the relative humidity (RH) is 100%, at 35°C the air can hold five times as much water vapour as at 10°C. At 50% RH, when the air is only half saturated, the capacity of the air to accept water from transpiring plants is still five times higher at 35°C than at 10°C. In other words, the water vapour deficit is five times greater at 35°C than at 10°C. Thus, if temperature is raised while water vapour

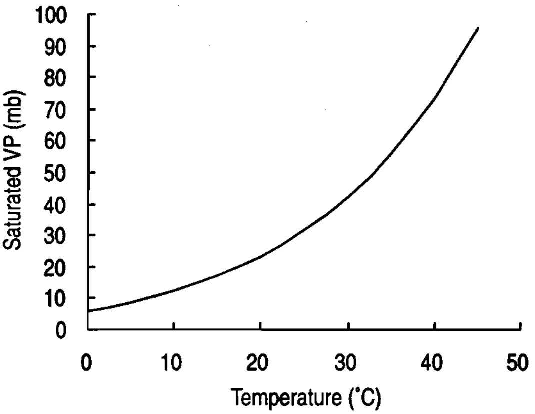

Figure 7. As air temperature increases, saturated vapour pressure of air also increases

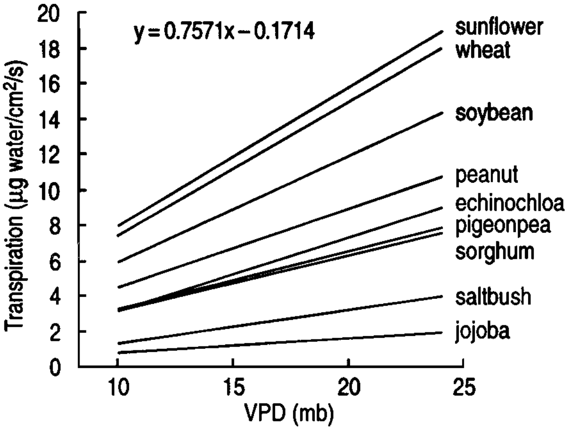

Figure 8. Transpiration rate of leaves increases linearly with an increase in vapour pressure deficit (VPD). Data from Rawson et al. (1977) and Rawson and Constable (1981)

content is held constant, the vapour pressure deficit (VPD) increases. This in turn increases transpiration rate if the stomata remain fully open. The relationship between transpiration and VPD for several species is shown in Figure 8. Points to note are:

- There is a linear relationship between VPD and transpiration. (Because of the curvilinearity of saturated vapour pressure versus temperature shown in Figure 7, transpiration is not linearly related to relative humidity.)
- Species differ in the slope of the relationship, but all intercepts are close to zero.
- The C3 grasses wheat and rice* have higher transpiration than the C4 species *Echinochloa crus-galli* (barnyard grass) and sorghum. (* Rice is not shown but is intermediate between soybean and peanut.) Desert species, like saltbush and jojoba, have low rates.

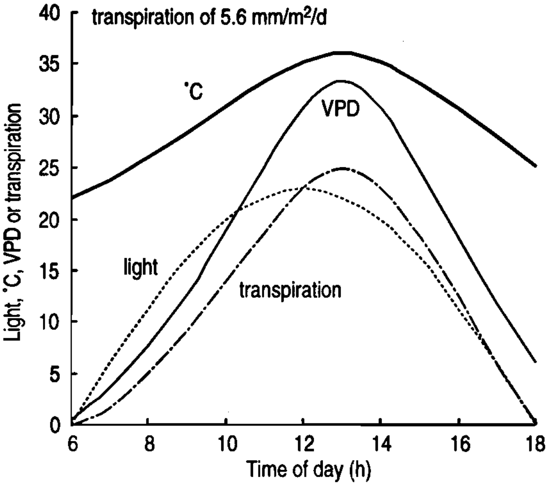

Figure 9. Weather data for a fictitious day with a vapour pressure (VP) of 26 mb, temperatures ranging between 22° and 36°C and totally clear skies. These combinations give a total transpiration from a wheat canopy with stomatal characteristics of the regression in Figure 4 of 5.6 mm/m²/d

The data were collected from plants that were not short of water, so there was no stomatal closure with increasing VPD in the studies.

What is the consequence of these relationships to sterility? If the hypothesis relating movement of boron into the plant and transpiration rate has any credence, then we can suggest that an increase in temperature, if it increases VPD, could actually reduce sterility, providing there is plentiful water available. Figure 9 shows some imaginary weather data for a hot location with temperatures ranging between 22° and 36°C during the daylight hours and with clear skies. A vapour pressure of 26 mb is assumed for the day. It shows that:

- vapour pressure deficit is driven by temperature (as is humidity)
- with constant vapour pressure, VPD and RH change substantially throughout the day (this has consequences for the time of day when measurements of weather variables should be collected in the field)

- transpiration, calculated from the VPD relationships in Figure 8, reached quite a high value equivalent to 5.6 mm water per day per m^2 of exposed leaf.

Under these conditions, water uptake, and therefore boron influx, would be considerable. In Figure 10, a different set of temperature conditions has been simulated, but the same VP of 26 mb is used. This moderate temperature range would be more typical of an overcast day. Using again the relationship of transpiration versus VPD of Figure 8, solely altering the temperature regime caused a reduction in daily transpiration to one-third. I have no idea whether this would potentially also reduce boron uptake by a similar proportion, but as a high proportion of boron uptake is associated with the transpiration stream (T. F. Neales, pers. comm.), it would almost certainly reduce it.

The estimates of crop transpiration from Figure 8 are gross overestimates as they are based on characteristics of young leaves that were fully exposed to radiation and in well stirred air with a negligible boundary layer. However, the relative effects of temperature and VPD will be acceptable estimates. As a rule of thumb, transpiration increases with leaf area towards a leaf area index of 4, but as the shape of the curve is a rectangular hyperbola, a leaf area index (LAI) of 2 would be transpiring at 75% to 80% of the saturation value and a LAI of 1 at about 50% (Frank X. Dunin, pers. comm.). Peak transpiration rates can exceed pan evaporation by up to 10% if the surface of the crop is rough, but transpiration rates would more normally be around 80% of pan evaporation.

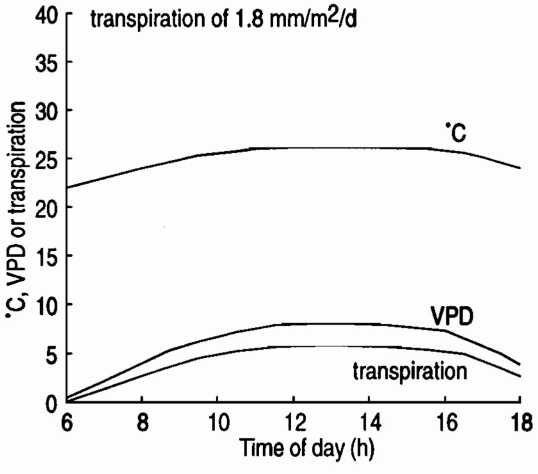

Figure 10. As for Fig. 9 except that temperatures were held between 22° and 26°C and transpiration fell to 1.8 mm/m^2/d

Irrigation affects transpiration. The effects depend on the water status of the crop, but the first effect from flood, furrow or sprinkler irrigation is to reduce air temperature and increase vapour pressure of the air. This decreases transpiration (Rawson et al. 1978). If vapour pressure is already high, transpiration could be reduced to very low levels with possible consequences for sterility if this occurs at sensitive plant phases. Furthermore, flood irrigation at these key phases could also reduce oxygen content of the soil and effectively result in brief waterlogging.

Frost damage—direct or indirect?

Frost damage can sterilise whole crops, and again the period between terminal spikelet and anthesis is very sensitive (Single 1971). Sterilisation occurs even though there can be little visible external sign of damage to the plant, particularly if the frosts are radiation frosts spanning only a few hours. The temperatures involved are likely to be between –4° and –7°C for the most dramatic effects, but less severe low temperatures (0° to –2°C) can have effects on photosynthesis lasting for several days (Marcellos 1977), which could arguably also result in partial sterility through carbon shortage at key stages.

It appears that low-temperature hardening can occur because field-grown plants can tolerate at least 2°C lower temperatures than glasshouse-grown plants without damage (Marcellos 1977). This is presumably because plants in the field can be exposed to diurnal variations in temperature of 15° to 20°C, whereas temperatures in glasshouses are usually more buffered. High temperature hardening can also occur. Santosh Kumari (pers. comm.) found that wheat plants that were grown at 21°/16°C until flag leaf emergence were fully sterilised when exposed to 35°/25°C and high VPDs during meiosis, and lost a high proportion of their photosynthetic tissues. By contrast, plants grown at 30°/25°C until the same stage suffered far less at 35°/25°C, especially if they had been subjected to water stress for one week. The two mechanisms of cold and high temperature hardening are likely to be different.

If it is suspected that frost or low night temperature might be causing sterility, it becomes vital to measure minimum temperatures at the surface of the crop canopy. Max./min. thermometers are probably adequate for this.

Relationship of humidity with VPD and transpiration rate

The hypothesis suggests relationships between boron uptake and transpiration rate. The relationship between transpiration rate and VPD has been described above. Most people make an estimate of humidity from measurements of relative humidity. Relative humidity (RH) is calculated either from the degree of contraction of an animal hair (horse or human in hydrographs), which is then related to the wetness of the air, or from the depression in temperature of a thermometer that has an evaporating surface wrapped around it (the wet bulb), compared with a dry thermometer (the dry bulb). The drier the air, the faster that water evaporates from the wet bulb, the more evaporative cooling that occurs and the cooler the wet bulb. In 100% RH, dry and wet bulbs are the same temperature.

Unfortunately, VPD and RH are not linearly related and so transpiration rate is not linearly related to RH. Figure 11 shows that at any RH, VPD differs with change in temperature. VPD can be calculated from RH using the following three equations:

SVP (mb) = a * EXP(b * dry bulb / (dry bulb + cc))

where a = 6.107799, b = 17.26939 and cc = 237.3

VP (mb) = SVP * RH * 0.01

VPD (mb) = SVP – VP

The related variable dew point =

cc * (LN(VP) – LN(a)) / (b – LN(VP) + LN (a))

By using tables of saturation vapour pressure (Table 4), values of RH and VPD can be calculated from dew point.

I am labouring these methods of measuring water vapour because it is important to be able to gain some estimate of transpiration (and possibly boron flux) from the instrumentation available.

Direct effects of humidity on sterility

I first became aware of the possible effects of high relative humidities on sterility when we grew wheat plants at high temperature in sunlit growth chambers in glasshouses. The single high temperature was achieved in one part of the study by cooling air taken from a hotter glasshouse, and in the other by taking air from a cooler house and then heating it. We (Bagga and Rawson 1977) had expected that, as the treatments were equivalent temperature, they would give the same grain set. Surprisingly for us, the Janak (HD 1982) plants with the heated air (higher VPD, lower RH) were more fertile than those grown in cooled air (higher RH), though some infertility occurred in all treatments in this genotype. By contrast, Kalyansona (Mexipak) showed little infertility regardless of treatment. This work was followed up (1976, unpublished data) by exposing Janak, Kalyansona and WW15 to differing humidities and 30°/20°C between flag leaf emergence and full ear emergence. High humidity (80%) fully sterilised Janak, again there was little effect on Kalyansona, and genotype WW15 was intermediate in response. All genotypes were fully fertile at 50% RH using the same temperature. We found that only the upper part of the plant including the flag leaves and boots needed to be exposed to high humidities to generate the effect. From memory, this would have been about half the plant leaf area. The lower part of the plant was held at 50% RH. These studies were done in artificially lit growth cabinets with about 400 µmol/m^2/s light, similar to the conditions used by Saini and Aspinall (1982b). Plants were all grown in a potting compost that had a basal application of nutrients plus slow-release, general-purpose pellets. Consequently, it is unlikely that boron was deficient in the medium, though it could have been deficient in the generative zones of the plants because of the treatment.

Tashiro and Wardlaw (1990) also examined the effects of humidity combined with high

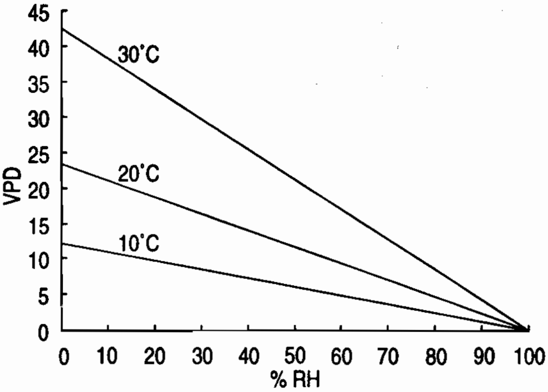

Figure 11. Relationships between relative humidity (RH) and vapour pressure deficit (VPD) at three temperatures

Table 4. Saturation vapour pressure (mb) of air at different temperatures

°C	0.0	0.1	0.2	0.3	0.4	0.5	0.6	0.7	0.8	0.9
0	6.11	6.15	6.20	6.24	6.29	6.33	6.38	6.43	6.47	6.52
1	6.57	6.61	6.66	6.71	6.76	6.81	6.86	6.91	6.96	7.01
2	7.06	7.11	7.16	7.21	7.26	7.31	7.36	7.42	7.47	7.52
3	7.58	7.63	7.69	7.74	7.80	7.85	7.91	7.96	8.02	8.08
4	8.13	8.19	8.25	8.31	8.36	8.42	8.48	8.54	8.60	8.66
5	8.72	8.78	8.85	8.91	8.97	9.03	9.09	9.16	9.22	9.29
6	9.35	9.42	9.48	9.55	9.61	9.68	9.75	9.81	9.88	9.95
7	10.02	10.09	10.16	10.23	10.30	10.37	10.44	10.51	10.58	10.65
8	10.73	10.80	10.87	10.95	11.02	11.10	11.17	11.25	11.33	11.40
9	11.48	11.56	11.64	11.71	11.79	11.87	11.95	12.03	12.12	12.20
10	12.28	12.36	12.44	12.53	12.61	12.70	12.78	12.87	12.95	13.04
11	13.13	13.21	13.30	13.39	13.48	13.57	13.66	13.75	13.84	13.93
12	14.02	14.12	14.21	14.30	14.40	14.49	14.59	14.69	14.78	14.88
13	14.98	15.07	15.17	15.27	15.37	15.47	15.57	15.68	15.78	15.88
14	15.98	16.09	16.19	16.30	16.40	16.51	16.62	16.73	16.83	16.94
15	17.05	17.16	17.27	17.38	17.50	17.61	17.72	17.84	17.95	18.07
16	18.18	18.30	18.42	18.53	18.65	18.77	18.89	19.01	19.13	19.25
17	19.38	19.50	19.62	19.75	19.87	20.00	20.12	20.25	20.38	20.51
18	20.64	20.77	20.90	21.03	21.16	21.30	21.43	21.56	21.70	21.84
19	21.97	22.11	22.25	22.39	22.53	22.67	22.81	22.95	23.09	23.24
20	23.38	23.53	23.67	23.82	23.97	24.11	24.26	24.41	24.56	24.72
21	24.87	25.02	25.18	25.33	25.49	25.64	25.80	25.96	26.12	26.28
22	26.44	26.60	26.76	26.92	27.09	27.25	27.42	27.59	27.75	27.92
23	28.09	28.26	28.43	28.61	28.78	28.95	29.13	29.30	29.48	29.66
24	29.84	30.02	30.20	30.38	30.56	30.74	30.93	31.11	31.30	31.49
25	31.67	31.86	32.05	32.25	32.44	32.63	32.82	33.02	33.22	33.41
26	33.61	33.81	34.01	34.21	34.41	34.62	34.82	35.03	35.23	35.44
27	35.65	35.86	36.07	36.28	36.50	36.71	36.92	37.14	37.36	37.58
28	37.80	38.02	38.24	38.46	38.68	38.91	39.14	39.36	39.59	39.82
29	40.05	40.28	40.52	40.75	40.99	41.22	41.46	41.70	41.94	42.18
30	42.43	42.67	42.92	43.16	43.41	43.66	43.91	44.16	44.41	44.67
31	44.92	45.18	45.44	45.69	45.95	46.22	46.48	46.74	47.01	47.27
32	47.54	47.81	48.08	48.35	48.63	48.90	49.18	49.46	49.73	50.01
33	50.30	50.58	50.86	51.15	51.44	51.72	52.01	52.30	52.60	52.89
34	53.19	53.48	53.78	54.08	54.38	54.69	54.99	55.30	55.60	55.91
35	56.22	56.53	56.84	57.16	57.48	57.79	58.11	58.43	58.75	59.08
36	59.40	59.73	60.06	60.39	60.72	61.05	61.39	61.72	62.06	62.40
37	62.74	63.08	63.43	63.77	64.12	64.47	64.82	65.17	65.53	65.88
38	66.24	66.60	66.96	67.32	67.69	68.05	68.42	68.79	69.16	69.53
39	69.91	70.28	70.66	71.04	71.42	71.80	72.19	72.58	72.96	73.36

temperature on floret fertility. They grew their wheat plants (Banks) in a glasshouse at 21°/16°C and transferred them to artificially lit cabinets for two days at five, three and one day before anthesis. There they were exposed to 36°/29°C and 35% or 50% RH (equivalent to VPs of 20 and 30 mb and VPDs of 40 and 30 mb respectively). The three-day stage (three days before anthesis) was most sensitive, but not to high temperature, only to higher RH (Fig. 12). Dawson and Wardlaw (1989) used Kalyansona in a similar study where plants were moved to 30°/25°C at head emergence until after anthesis. Their RHs were 34% and 84% (VPs of 14 and 36 mb and VPDs of 28 and 7 mb). The higher RH combined with high temperature resulted in 14% increased sterility of central spikelets. There was no effect of different humidities on sterility at 18°/13°C.

Different responses of genotypes to high humidity

Taken together, the results above suggest that there are genotype differences not only in response to high temperature but also in response to high humidity associated with high temperature. Kalyansona has proved in several different studies to be stable, whereas Janak is unstable. Whether the differences are related to differences in the ability of genotypes to maintain transpiration at high RH is not known. As in the Bagga and Rawson studies, plants were not short of boron in the root medium as water and Hoaglands nutrient solution were applied daily. However, it is quite possible that the boron-sensitive lines are also humidity-sensitive. This has to be determined.

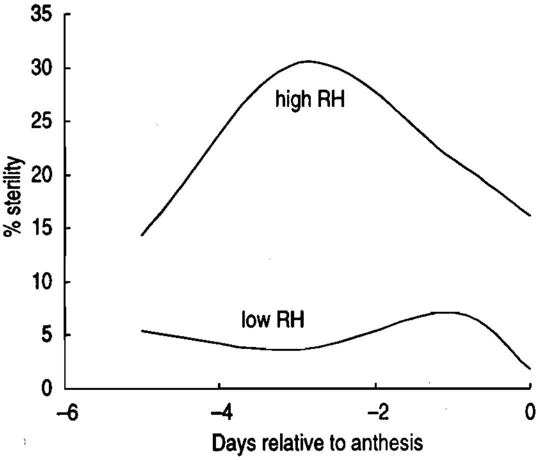

Figure 12. Humidity effects in combination with high temperature (36°/29°C) for two days at various stages on floret sterility in Banks wheat. The greatest degree of sterility was achieved at high RH and high temperature three days before anthesis (from Tashiro and Wardlaw 1990)

Low and high radiation effects on sterility and association with other weather variables

Anecdotal evidence indicates that low radiation in combination with high temperature could increase sterility. The effects of low radiation on grain numbers have been discussed above, but I can find no data where effects on sterility were considered. It is not difficult to speculate why low radiation might result in sterility. First, it will reduce carbon availability for growth. However, it would be surprising if this were a main cause of sterility as there is usually sufficient carbon in store or in transit to keep growth processes going for one to two days. If there were a link between boron movement and carbon concentration gradients (that is, if boron were moved in the phloem), low radiation could perhaps work to limit boron levels at the floret sites. Again this seems unlikely. However, there might be direct effects of radiation on transpiration rate.

Low and high radiation effects on transpiration via stomatal aperture

I would suspect that low radiation coupled with high temperatures might be having its effect on sterility via transpiration rate, which in turn might influence boron uptake. Wheat stomata are essentially closed in the dark, but even then there can be some loss of water through them and through the cuticle in dry climates at night (Rawson and Clarke 1988). In the light, the stomata open, and open wider with increase in light intensity (Fig. 13). The stomata of young leaves respond to light almost up to full sunlight, but as leaves age, their stomata tend to reach a plateau at progressively lower light levels. Leaves of different ages differ little in response up to about 400 μmol/m²/s light.

The effect of this stomatal response on transpiration over a full day can be quite substantial, but the size of the effect depends on whether the day is clear or cloudy. Calculating transpiration patterns for a completely clear day

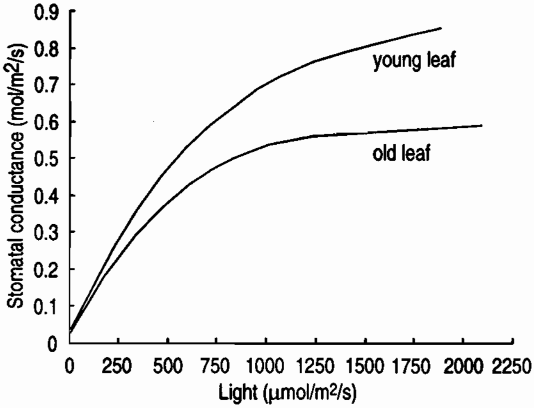

Figure 13. Effects of light and leaf age on stomatal conductance in wheat. As leaves age, their stomata become less responsive (from Rawson 1986b)

for fully open stomata gives a transpiration rate of 5.6 mm/d (Fig. 9). Recalculating for stomata with the light response of Figure 13 gives a transpiration rate of 5.2 mm/d, only 7% less. Thus on a sunny day the effect is negligible. However, on a cloudy day the effects can be significant. For example, on a day with the same VPDs as in the previous example, which starts sunny, but then becomes cloudy with light reducing to 400 µmol/m²/s, we find that if we allow the stomata to respond to light, the stomatal effect reduces transpiration from 5.6 to 3.4 mm/d or by 40%. This value of 400 µmol/m²/s is a typical light level for days of light cloud with full cover.

On days of low VPD such as in Figure 10, when transpiration is already limited by VPD, stomatal closure in response to low light could reduce transpiration to extremely low levels. These types of days could have heavy cloud cover in early afternoon that would reduce radiation from potentially 2000 to < 100 µmol/m²/s. We have recorded light levels before thunderstorms down to 40 µmol/m²/s, when the stomata could be only 10% to 12% open because of light constraints. On such days, if boron were already low in the soil, it could become limiting in the plant for developmental processes.

High radiation, if coupled with shortage of soil water, could equally have detrimental effects by leading to open stomata and high rates of water loss (depending on VPDs) until water stress resulted in closed stomata. This type of situation has been well described elsewhere (for example, Rawson et al. 1978; Rawson and Constable 1981). This could also result in sterility (Saini and Aspinall 1982b).

Just as there are differences between leaf ages in their stomatal control and maximum apertures, there are differences between genotypes. Dr A. G. Condon has published details of these in association with other scientists in several papers. He has demonstrated that Australian genotypes derived from WW15 tend to much lower conductances than other genotypes. If the hypothesis relating transpiration rate and boron uptake has any support, *genotypes with high conductance (potentially fast transpiration) would be less likely to be sterile.*

There are general associations between radiation and other weather variables. In effect, radiation drives the other variables. Thus, on clear days, temperature drops at night, as there are no clouds to retain the long-wave energy stored during the day. If the air temperature falls to a level where the air becomes saturated with water (see Table 4 of saturation vapour pressure and Figure 7 of saturated VP versus temperature) and there are surfaces that are at or below this temperature, dew will form. During the following clear day, this dew will become vapour as temperature rises and the capacity of the air to hold water vapour increases. Temperature will rise to relatively high levels as the sun warms up the surfaces, and VPD will increase. Under cloudy conditions, however, the maximum to minimum temperature range is much less, with generally warmer nights and cooler days, and daytime VPD will be lower. However, each location is not independent, and weather fronts move, so there will be occasions when there will be relatively *high temperature and low radiation associated with high vapour pressures and low VPD.* It would seem, according to observations and the hypothesis, that these combinations are likely to result in sterility possibly because transpiration rates are very low and development is proceeding very quickly.

Conclusions

The causes of sterility are going to remain elusive if we fail to describe the environment and the plant in sufficient detail in our field studies. Unfortunately, sterility becomes obvious only days to weeks after the combination of events that caused it. So retrospective data analyses are required to identify the causes. It would seem that sterility can be caused by many factors of the environment, and by these factors in various combinations, and that genotypes differ in their sensitivity to the different factors. So pinning down the cause of sterility is no easy task. Because we tend to expect or hope that single factors cause plant problems we often tend to simplify our experimentation on plants. Sterility in wheat is one case in which we have to assume that the answer is complex, so we have to measure almost anything that might be even vaguely associated with sterility.

The hypothesis linking sterility to the movement of trace elements into and through the plant during the period spanning flag leaf ligule emergence to anthesis unifies several apparently interacting environmental effects. This is because of the complex effects of the environment on transpiration rate and the linked dependence of movement of boron with that. If we can come to a consensus on how to describe sterility, and what aspects of the soil and aerial environment we need to measure and when, and can provide a network of experiments that must give us every possible combination of environmental variables at key stages, we will come close to defining the problem. Overlay this with a range of genotypes with reputed different sensitivities, and we will stand a good chance of answering the question 'what causes sterility?'

Acknowledgments

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Boron and Plant Reproductive Development

Benjavan Rerkasem*

Abstract

Boron deficiency affects growth in many plant species, although the degree and the timing of the onset of the visible effects differ. In cereals, reproductive development can be depressed without any apparent effect on vegetative development. The problem is normally expressed in the development of internal floral parts and the fertilisation process, often with no apparent effect on the external structure of the flower. It is likely, but not established, that reproductive development requires higher boron concentrations than vegetative development. Data in this paper show five to six times higher concentrations in wheat anthers than in the whole ear. A high concentration was also found in the carpel, although not as high as in the anther. Pollen germination and pollen tube growth are strongly influenced by external boron supply.

Plant Reproductive Responses to Boron

The ultimate effect of boron deficiency on plant reproductive development is the depression of the number of fruits or seeds set per plant and fruit or seed yield.

In red clover, boron deficiency decreased the number of flowers and seed and seed yield (Sherrell 1983). Subterranean clover growing in a low boron soil flowered only sparsely, with fewer flowers per inflorescence (Dear and Lipsett 1987). In black gram, boron deficiency caused premature shedding of flower buds, flowers and young pods, thus decreasing the number of pods set (Rerkasem et al. 1988; Predisripipat 1988). Once the pods were set, the number of seeds in the pods was less sensitive to boron deficiency.

Under a condition of boron deficiency, rice set fewer grains per head (Garg et al. 1979). In maize, boron deficiency depressed grain formation but had no apparent effect on the structural growth of the silk, anthers or pollen grain (Vaughan 1977). In wheat and barley, the number of grains per spikelet can be depressed by boron deficiency without any apparent effect on the number of ears formed or the number of spikelets per ear (Rerkasem et al. 1989; Rerkasem and Jamjod 1989).

There seems to be a difference between legumes and cereals in the response of their reproductive development to boron deficiency. In legumes, the first effect is on external structural development of the flowers. In cereals, the problem is normally expressed in the development of internal floral parts and the fertilisation process, often with no apparent effect on the external structure of the flower.

Reproductive Development Process and Boron

The process of reproductive development begins with flower initiation, followed by flower formation, which includes development of floral parts, and is completed with fertilisation. The effect of other nutrients on flower initiation is well known; for example, nitrogen in apples (Lüdders and Bünemann 1970), or phosphorus in apples (Bould and Parfitt 1973), tomato (Menary and Van Staden 1976) or wheat (Rahman and Wilson 1977). A study in India reported that a boron application increased the number of female flowers and decreased the number of male flowers in cucumber (Maurya 1987).

Once floral initiation has started, boron deficiency can affect further development of the flower. Some effects can act directly on the development of the floral parts, but others can be indirect. An example of an indirect effect is the development of corky and brittle stem in sunflower, which can cause it to break just below the flower head, and so the whole flower is lost (Rerkasem 1986; Blamey et al. 1987). It is not

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known if the shedding of flower buds, flowers and young pods in boron-deficient black gram (Predisripipat 1988; Noppakoonwong 1993) is the effect of boron deficiency on the senescence process or on flower development.

The effect of boron on the development of the pollen grain has been reported for many species, including wheat (Li et al. 1978; Rerkasem et al. 1989), maize (Agarwala et al. 1981) and rice (Garg et al. 1979). In general, boron deficiency produces pollen grains that are small and misshapen and do not accumulate starch (that is, do not stain with iodine). Pollen that appears to have developed normally can still have been affected by boron deficiency (Vaughan 1977; Cheng and Rerkasem 1993).

The process of fertilisation involves the germination of the pollen grain and the growth of the pollen tube down the style into the ovary.

Pollen germination and pollen tube growth are most strongly influenced by external boron supply. Many in vitro studies have shown a requirement of external boron for germination and growth of pollen tube; for example, in lily (Dickinson 1978), wheat (Cheng and McComb 1992; Cheng and Rerkasem 1993) and maize (Agarwala et al. 1981). In vivo, pollen germination and tube growth can be limited by boron deficiency in the stigma and style. In maize, grain set failed completely with silk boron concentration at 2.4 mg/kg dry weight or less (Vaughan 1977). Manual pollination of wheat with boron-sufficient pollen on boron-deficient pistils resulted in only 28% grain set, compared with 94% grain set on boron-sufficient pistils (Rerkasem et al. 1993).

Boron Requirement for Reproductive Development

It is commonly believed, as in a general statement made by Marschner (1991), that 'the supply of boron required for seed and grain production is usually higher than that needed for vegetative growth.' That is, concentrations of boron that have no apparent effect on vegetative development can depress reproductive development. Many studies support this statement in a general way; for example, in maize (Vaughan 1977), white clover, red clover (Sherrell 1983), subterranean clover (Dear and Lipsett 1987), black gram (Rerkasem et al. 1988) and wheat and barley (Rerkasem et al. 1989; Rerkasem and Jamjod 1989).

Few data exist, however, to indicate that boron requirement for reproductive development really is higher than for vegetative growth. For example, a boron concentration of 10 mg/kg in the blade opposite and below the cob at tasselling has been considered critical for maximum yield of the whole plant (Melsted et al. 1969), yet maize pollen containing about the same amount of boron, at 10.8 mg/kg, exhibited no evidence of boron deficiency (Agarwala et al. 1981), and only 4 mg/kg in the silk was sufficient for maximum fertilisation and grain set (Vaughan 1977). Furthermore, in the study by Agarwala et al. (1981), maize plants with pollen showing some effects of boron deficiency (lower number of pollen per anther and lower percentage pollen germination) exhibited some vegetative response to boron deficiency.

On the other hand, our own preliminary analysis (Rerkasem and Lordkaew, unpublished) shows a concentration of boron in wheat anthers five to six times that in the whole ear (Table 1). High concentrations of boron were also found in the carpel, although not as high as in the anther. In our previous experience, sterility was associated with boron concentrations in emerged wheat ears of 2 to 5 mg/kg (Rerkasem et al. 1989; Rerkasem and Lordkaew 1992).

Römheld and Marschner (1991) noted that boron has a special role in the fertilisation process. There is a specific boron requirement for pollen tube growth, in which callose formed at the pollen tube – style interface as the result of the pollen tube 'invasion' is physiologically inactivated by the formation of borate–callose complexes (Lewis 1980). Marschner (1991) also suggested that extra boron is needed to maintain efficient oxidation of phenols formed in the 'invasion' of the style by the germinating pollen tube.

Does Plant Reproductive Development Require More Boron Than Vegetative Growth?

There is insufficient information yet to indicate that reproductive development does require more boron than vegetative growth. Observations that flower development and seed and grain production are much more depressed than vegetative growth when boron is deficient can be explained by one or more of the following:

- The boron requirement for reproductive

Table 1. Boron concentrations (mg/kg) in different parts of the wheat ear at ear emergence and at anthesis in five wheat cultivars. Each number is a mean of three replicate plots of field-grown plants

Genotype	Ear emerged		At anthesis	
	Whole ear	Anthers	Whole ear	Carpel
SW-41	2.6	14.0	2.6	6.8
Glenaro 81	3.7	14.3	2.7	9.2
Glennson	2.9	18.0	2.5	8.9
Nesser	3.4	16.7	3.8	10.9
Seri 82	3.5	15.3	2.7	6.7
SE	0.6	5.2	0.7	2.0

development is greater than for vegetative growth.

- The supply of boron to the reproductive tissue is more easily interrupted.
- The rate of supply of boron to the reproductive tissue is insufficient to meet demand because of the rapid growth of reproductive organs and their limited ability to transpire water.

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Tissue Boron

Benjavan Rerkasem and S. Lordkaew*

Abstract

This field experiment set out to examine the relationship between boron in various parts of the wheat ear and flag leaf, and grain set. Four rates of B were used: 0, 0.5, 1.0 and 2.0 kg/ha. Two genotypes were sown: SW-41, which is sensitive to B deficiency, and Fang 60, which is tolerant. Tissue B was determined at ear emergence in anthers, carpel, whole ear and flag leaf. Grain set was assessed in unbagged and bagged ears to evaluate effects of B and cross-pollination on grain set.

B concentration in the whole ear of SW-41 was about half that in the flag leaf. However, within the ear, B was much more concentrated in the anthers and carpels than in the remainder of the ear or even the flag leaf. The variation in grain set with soil B concentrations was more closely related to anther and carpel B than to flag leaf and ear B. In the presence of Fang 60, bagging significantly depressed grain set in SW-41, indicating a major effect of Fang 60 as a pollen donor. There was a clear indication of the influence of soil B concentrations on cross-pollination. The relative difference in number of grains per ear between bagged and unbagged ears was greatest at lowest soil B and virtually disappeared at highest soil B.

Materials and Methods

Fang 60 and SW-41 were sown in a field at Chiang Mai University Field Station. The field had four concentrations of B (0, 0.5, 1.0 and 2.0 kg/ha, designated B0, B1, B2, B3) applied to fresh plots in three successive years (1989, 1990, 1991). There were four replicates. The years were in main plots, B rates in subplots, and the two genotypes in sub-sub-plots. The subplots were 3 m × 10 m. Rows were 25 cm apart and ran the length of the subplot. Each subsubplot comprised six rows, each 10 m long, of Fang 60 or SW-41. See Rerkasem and Loneragan (1994) for details of the treatments.

The soil is a Typic Tropaqualf sandy loam with an original hot-water-soluble boron concentration of 0.10 to 0.14 mg/kg.

At ear emergence, the tissues were sampled from 50 randomly selected ears and analysed separately as:

- anthers (may or may not include filaments)
- carpels (style and ovary)
- the remaining glumes, chaff etc.
- flag leaf.

As the ears emerged, up to a hundred ears in each subplot of SW-41 were bagged to prevent cross-pollination. At maturity, grain set was determined from these and from a hundred randomly sampled ears that were not bagged.

Results and Discussion

Effects of the year of B application, either as main effect or in interaction with B, were not significant. All tabulated data presented here are means of the three years.

Residual effects of the B treatments were still very clear after three years on SW-41. During anthesis, SW-41 was showing the typical sterility symptom of gaping glumes, giving it a transparent look, especially in B0 and B1. Fang 60, by contrast, had very few ears with glumes that were gaping at anthesis.

Grain set

Fang 60 began flowering two to three days before SW-41, but both genotypes were at anthesis at largely the same time.

Only a few ears of Fang 60 were bagged. Average grain set index (GSI) in bagged ears in B0 was 85.2%. Average GSI in unbagged ears ranged from 91.0% in B2 to 95.1% in B3. On the whole there was little indication of B deficiency at anthesis or in grain set in Fang 60.

Grain set in SW-41 responded strongly to an increasing rate of B application. Grain set, as GSI

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Table 1. Effect of bagging on grain set in SW-41 in the presence of Fang 60, at four concentrations of soil B

B treatment	GSI (%)			Grains/ear		
	Bagged	Unbagged	% difference	Bagged	Unbagged	% difference
B0	22.3	41.3	85.2	6.98	11.8	69.1
B1	36.3	60.8	67.5	9.82	19.5	98.6
B2	46.4	72.4	56.0	15.2	23.2	52.6
B3	59.7	77.4	29.6	21.4	25.6	19.6
SE	6.1			3.49		

and number of grains per ear, was much greater in unbagged ears than in bagged ears (Table 1). This indicates a major effect of cross-pollination in the presence of a pollen donor, Fang 60.

There was a clear indication of the influence of soil B concentrations on cross-pollination. The difference in number of grains per ear between bagged and unbagged ears was about the same in B0 and B1, in which unbagged set about twice as many grains as bagged. The difference declined with further increase in soil B and virtually disappeared in B3.

In SW-41 in B0 and B1, there appeared to be a more severe effect of B deficiency on the pollen than on the carpel. This was indicated by the doubling of grain set when cross-pollination was allowed. This confirms our earlier findings that grain set in B-deficient ears was increased by manual pollination with fertile pollen (Rerkasem et al. 1993).

B concentration in different parts of the wheat ear

B concentration in the whole ear of SW-41 was about half that in the flag leaf (Table 2). However, within the ear, the B was much more concentrated in the actual reproductive parts (anthers and carpel) than in the whole ear or in the flag leaf (Table 2).

The variation in grain set with soil B concentrations was more closely related to anther and carpel B than to flag leaf and ear B. For example, grain set in bagged ears in B0 was only one-third of that in B3, but their flag leaf and whole ear B were essentially indistinguishable. Anther and carpel B, on the other hand, were correspondingly and significantly lower in B0 and B1 (Table 2).

Ears containing 7 to 8 mg/kg B in the anthers responded to cross-pollination, as did ears with carpels with 5 to 6 mg/kg B. These results seem to suggest that effective anthers require more B (> 8 mg/kg) than receptive carpels (< 6 mg/kg). Carpels, in turn, could require more B than vegetative growth. No indication of a B effect was observed on vegetative growth (Table 3).

The anthers and carpel represent only about 2% each of the ear dry weight (Table 3), but they account for a much larger share of B: 6% to 7% in anthers and 4% to 5% in carpels of the total B in the whole ear (Table 4).

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Table 2. Effect of bagging on grain set in SW-41 in the presence of Fang 60, at four concentrations of soil B

Treatment	B (mg/kg) in			
	Flag leaf	Anthers	Carpel	Whole ear
B0	4.7	7.5	5.5	2.2
B1	4.1	7.0	5.1	2.5
B2	4.4	8.3	5.7	3.1
B3	4.5	9.4	7.5	2.9
SE	0.6	1.0	0.8	0.4

Table 3. Effects of B on distribution of dry weight in different parts of the ear and on number of spikelets per ear

B treatment	% dry weight in		
	Anthers	Carpel	Chaff
B0	1.8	1.8	96.4
B1	1.9	2.2	95.9
B2	2.0	1.9	96.1
B3	2.2	1.8	96.0
Sig. diff. ($p < 0.05$)	NS	NS	NS

Table 4. Distribution of B in different parts of the ear

B treatment	% B in		
	Anthers	Carpel	Chaff
B0	6.8	4.6	89.2
B1	6.1	4.9	89.0
B2	5.8	3.7	90.5
B3	7.1	4.5	88.4
Sig. diff. ($p < 0.05$)	NS	NS	NS
SE	2.1	1.6	3.6

Effect of Fertilizers and Boron on Yield and Boron Uptake in Wheat

Krishna B. Karki*

Abstract

An experiment was conducted on two low-fertility soils (Rhodic Ustochrepts and Ochric Fluvaquents). The main objective was to evaluate the effects of organic manure and boron on growth and yield in wheat. Four fertilizer treatments were used as main plots (control with no added fertilizer, farmyard manure (FYM), town compost and NPK mineral fertilizer), and two levels of boron were included as subplot treatments (control and borax 2.5 kg/ha). Soil samples throughout the soil profile were collected before the experiment.

The NPK treatment produced the highest grain yield at both sites. Town compost plots yielded more than the FYM plots at Kalleritar, but less at Baireni. Application of boron improved grain yield in the well drained, medium-textured soil at Kalleritar. In the poorly drained and light-textured soils at Baireni, however, further investigation is needed before boron application can be recommended.

Neither fertilizers nor boron increased the concentration of boron in the plants, but concentrations were all above the minimum needed.

THE agricultural development strategy of Nepal seeks to transform the traditional subsistence agriculture. Lands with access to assured irrigation are cultivated throughout the year using nutrient-demanding crops such as rice, wheat and maize in rotation. High-yielding crop varieties are cultivated every year without replenishing the nutrients they removed. Nepalese farmers use high doses of organic manure such as farmyard manure and compost to fertilize their land (Upreti et al. 1989). In the traditional farming system, local varieties were less responsive to mineral fertilizers, so the use of mineral fertilizers was not common.

Rapid population growth and increased demand for food necessitated adoption of the new high-yielding varieties, combined with higher intensities of cropping. Such intensification required more and more plant nutrients.

Food production from existing farmland has been insufficient and so cultivation has extended onto marginal lands. Mining of soil nutrients has continued and crop production has plateaued or even decreased. This decrease is due mainly to the use of low application rates of fertilizers, which has led to deficiencies of both macro- and micronutrients. This in turn has led to sterility of some cereals, which has been associated with deficiencies of some essential elements such as boron (Scherchan and Bania 1991; Hobbs et al. 1987).

With the objective of examining the effect on wheat yields of various fertilizer combinations, and to observe the response of boron alone and in association with locally available organic manure, an experiment was conducted on two sites in the Dhading Districts of Nepal.

Materials and Methods

The soils on which the experiment was conducted were classified as Rhodic Ustochrepts and Ochric Fluvaquents. The experiment was laid out in a factorial design using plots of 4 m × 5 m. The crop was sown in November 1991. The treatments were as follows:

Factor A

1. Control
2. Farm yard manure (FYM 28 t/ha)
3. Town compost (28 t/ha)
4. Mineral fertilizer (Complesal®, 20:20:0, + KCl)

Factor B

1. Control
2. B (2.5 kg/ha as borax)

The organic manures were applied two weeks before sowing and incorporated into the soil the

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same day. The KCl and the borax were applied at sowing. Side-dressings of urea were applied, half at sowing and half 35 days later.

Soil samples were collected for laboratory analysis alongside the experimental plots. Plant samples were collected at flowering; ten plants were selected randomly from each plot. The above-ground parts of the plants were clipped with stainless steel tools, washed thoroughly with distilled water, dried in a hot air oven at 50°C, ground and then stored for analysis. At maturity, in April 1992, the crop was harvested and dried in the sun. Each plot was threshed separately. Clean seeds were weighed at 14% moisture content and the results were statistically analysed.

Soil pH was determined in a 1:2.5 soil–water paste. The soil samples were digested in aqua regia for total element analysis or in acid ammonium acetate (AAAc) for available nutrient analysis. The plant samples were digested in triacid mixture. Total N and C were determined in a CNS combustion analyser. Other elements were determined by ICP. Soil particles were separated by pipette.

Results

The soil profile at Kalleritar is deep and well drained but the profile at Baireni is comparatively shallow and poorly drained. At Kalleritar, silt dominates the particle size distribution in the surface layers (Table 1) but decreases with depth. The clay fraction increases with depth and the sand shows no clear trends. At Baireni, sand dominates the whole profile. There is virtually no clay in the soil except in the upper layer.

The pH of the soil at both sites was slightly acidic to almost neutral. The available N, C and P in both soil profiles was low (Table 2). These soils were rated as of low fertility.

The compost and farmyard manure contained sufficient total P, Ca, Mg, and K (Table 3). The boron content of farmyard manure at both sites was higher than in town compost, especially that from Kalleritar, though it was not considered high enough to create problems.

The analysis of results from the fertilizer treatments at Kalleritar showed that application of mineral fertilizer produced highly significant yield increases relative to the control (Table 4). Grain yields of plots treated with organic manures were not statistically greater than those of untreated plots. Low temperatures during the prime growth period of wheat in Nepal inhibit mineralisation of nutrients from organic materials (Suzuki et al. 1990), but higher crop yields in subsequent crops could be due to later mineralisation (Sharma et al. 1987). The organic treatments could therefore have shown higher yields the following year.

At the Baireni site, the mineral fertilizer produced the highest yield. Farmyard manure produced the second-highest yield, significantly greater than the town compost.

The importance of boron in the plant system has been highlighted by many authors. In the context of Nepal, application of boron in various experiments has produced positive responses (Khatri Chhetri and Shimire 1992; Sherchan and Bania 1991). In this experiment, B application at the Kalleritar site gave a slight positive response, but not at Baireni (Table 5).

Comparing the results of all the combination treatments, the NPK + B and NPK alone produced the highest yields (Table 6). Application of B with farmyard manure and with town compost at Kalleritar produced higher yields than farmyard manure and town compost without B. Though application of boron proved beneficial at Kalleritar, at Baireni it reduced yield. This reduction might have been due to the poor internal drainage of the soil. In lighttextured soil, adsorption of boron is low. Unexpected winter rain fell in January and February at Baireni.

Table 1. Particle size distribution in the soil of Kalleritar and Baireni (%)

Depth (cm)	Sand	Silt	Clay	Texture
Kalleritar				
0–10	20.3	61.6	18.0	Silt loam
10–31	19.0	61.0	20.0	Silt loam
31–54	29.0	44.5	26.0	Loam
54–80	30.0	32.0	38.0	Clay loam
80–140	27.0	28.5	44.0	Clay loam
Baireni				
0–14	62.5	34.5	3.0	Sandy loam
14–35	58.0	41.0	1.0	Sandy loam
35–56	69.5	30.0	0.5	Sandy loam
56–80	83.0	16.5	0.5	Loamy sand

Table 2. Soil pH, C, N and available macronutrients (mg/kg)

Depth (cm)	pH	C (%)	N (%)	P (mg/kg)	Ca (mg/kg)	Mg (mg/kg)	K (mg/kg)	CEC meq/100 g
Kalleritar								
0–10	6.75	1.20	0.065	136	1749	34.4	157	12.2
10–31	7.04	0.78	0.045	61.2	1736	33.7	120	11.7
31–54	6.84	0.58	0.030	29.8	1440	27.3	132	9.79
54–54	6.68	0.39	0.025	42.2	1243	31.5	180	9.03
84–140	6.80	0.23	0.020	9.83	1054	34.4	194	8.76
Baireni								
0–14	6.12	0.73	0.035	32.0	880	8.45	59	8.76
14–35	6.58	0.58	0.031	38.8	1217	15.8	207	11.4
35–54	6.75	0.27	0.025	29.4	788	6.84	52	10.1
54–80	6.78	0.14	0.006	27.7	401	3.33	35	4.28

Table 3. C, N and total nutrients in the organic manures (mg/kg)

Materials	C (%)	N (%)	P (mg/kg)	Ca (mg/kg)	Mg (mg/kg)	K (mg/kg)	B (mg/kg)
Town compost	14.7	0.45	3090	15400	4430	7870	10.9
FYM Kalleritar	14.5	0.97	4240	11400	9780	17900	38.8
FYM Baireni	5.8	1.10	4170	11400	8680	17900	18.0

Table 4. Wheat grain yield as affected by fertilizer application

Treatments	Grain yields at Kalleritar (kg/ha)	% increase over control	Grain yields at Baireni (kg/ha)	% increase over control
Control	1193		550	
FYM	1477	19	1429	260
Town compost	1610	26	897	63
NPK	3897	269	5205	846
CV%	8.8		10.5	
Sig. diff.	94		124	

At Kalleritar, the control plants (without any fertilizers) had a higher tissue B content than the fertilizer-treated plants (Table 7). At Baireni, the differences were very small, though the trend was similar.

The effect of boron on boron uptake followed the same trend in all treatments at Kalleritar: boron application resulted in lower tissue boron concentrations. At Baireni, the results were variable (Tables 8 and 9).

In spite of lower boron concentrations in the boron-treated plants, in all plants the concentration was much higher than the concentration at which deficiency symptoms appear. Similar results were published by Mengel and Kirkby (1979) and Sillanpaa (1982). The lower concentration of B in the crops was possibly due to a dilution–concentration phenomenon (Sillanpaa 1982), in which content had risen but plants had grown, so reducing the concentration.

Table 5. Wheat grain yield as affected by boron application

Treatments	Grain yields at Kalleritar (kg/ha)	% increase over control	Grain yields at Baireni (kg/ha)	% increase over control
Control	1931		1518	
Boron	2079	7.7	1414	–6.9

Table 6. Wheat grain yield as affected by application of fertilizers and boron

Treatments	Grain yields at Kalleritar (kg/ha)	% increase over control	Grain yields at Baireni (kg/ha)	% increase over control
Control	1033		575	
Control + B	1208	17	766	33
FYM	1380	34	1316	128
FYM + B	1566	52	1100	91
Town compost	1516	47	1216	111
Town compost + B	1650	60	850	48
NPK	3791	267	2966	415
NPK + B	3891	277	2940	411

Table 7. Effect of fertilizer application on boron content of wheat plants

Treatments	B (mg/kg) at Kalleritar	B (mg/kg) at Baireni
Control	12.1	10.7
FYM	5.27	9.90
Town compost	7.48	10.5
NPK	5.59	9.78

Table 8. Effect of boron application on boron uptake in wheat plants

Treatments	B (mg/kg) at Kalleritar	B (mg/kg) at Baireni
Control	12.8	3.11
Boron	6.27	6.05

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Table 9. Effect of fertilizers and boron on boron content of wheat plants

Treatments	B (mg/kg) at Kalleritar	B (mg/kg) at Baireni
Control	17.1	12.8
Control + B	8.01	16.6
FYM	20.4	7.14
FYM + B	2.08	7.02
Town compost	3.10	5.91
Town compost + B	0.85	5.40
NPK	7.70	16.9
NPK + B	10.2	10.5

Field studies within the project

Influence of Seeding Date, Genotype and Boron on Sterility of Wheat in Bangladesh

M. Saifuzzaman*

Abstract

Wheat sterility has occurred in some years in growers' fields in the north-west of Bangladesh, causing devastating yield reductions. An experiment was organised to understand the reasons for sterility in wheat in Bangladesh. It was conducted during the 1994–95 wheat-growing season at the Wheat Research Centre, Dinajpur. Three genotypes of varying degrees of sterility associated with boron deficiency were sown at three planting dates to vary the growing environment. Seeding dates, genotypes and their interactions significantly influenced the dates and timing of phenological events (such as days to heading and anthesis). There was no significant influence of boron on sterility or basal floret fertility. Sterility varied only with genotypes; interactions with boron and seeding date were not significant. Significant differences were observed between genotypes, seeding dates and their interaction on yields and on most variables that contribute to yield. Boron concentrations in the flag leaf at booting were highly correlated with soil-applied boron.

STERILITY in wheat was first observed and reported in growers' fields in 1987 in north-western Bangladesh, and has since been reported in other parts of the country (Saifuzzaman 1994). Sterility was first observed in the Mexican wheat variety Tanori 71 in the Thakurgaon seed increase farm of the Bangladesh Agricultural Development Corporation in 1974 (Razzaque, pers. comm.). Grain set failure or sterility in wheat is an important yield constraint in the rice–wheat system of South and South-east Asian countries including Bangladesh in some years (Mann and Rerkasem 1992).

In Bangladesh, wheat was introduced as a new crop in the early 1970s for large-scale cultivation and it has become the second most important cereal crop after rice. After its introduction, the area and production increased sharply (Saifuzzaman and Meisner, these Proceedings). During 1994–95, the crop was grown on an area of about 677 000 hectares, producing nearly 1.4 million tonnes of grain (BARI 1995). The soils of sterility-prone areas are mostly sandy loam with a low pH (4.8 to 5.8). These soils are thus likely to be boron-deficient (Palkovics and Gyori 1984). The soil is also poor in organic matter, nitrogen and zinc (Jahiruddin 1991).

Many researchers have found that low soil boron causes sterility in wheat (Singh et al. 1976; Ganguly 1979; Li et al. 1978; da Silva and da Andrade 1983; Sthapit et al. 1989; Rerkasem et al. 1989). Deficiency of copper has also been found to cause sterility (Graham 1975; Galrao and Sousa 1988; Grendon 1991). Besides these nutrient deficiencies, environmental conditions can cause sterility. These include high humidity and low light (Willey and Holliday 1971), high temperature (Saini and Aspinall 1982; Saini et al. 1983), low night temperature (Kim et al. 1985; Subedi et al. 1993), water stress (Bingham 1966; Fischer 1970; Saini and Aspinall 1981) and waterlogging (Misra et al. 1992). Additionally, some genotypes are prone to sterility (Chatterjee et al. 1980; Rerkasem 1990; Subedi et al. 1993).

Until now, no single factors have been identified as conclusively causing wheat sterility in Bangladesh. The present research program was developed, with the assistance of the Australian Centre for International Agricultural Research, to determine the causes in several South and South-east Asian countries. This paper briefly reports the findings of the experiment conducted in Bangladesh, especially focusing on the interactions and correlations between the sowing dates, boron levels and genotypes and their effects on wheat sterility.

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Materials and Methods

The experiment was conducted in an experimental field of the Wheat Research Centre, Dinajpur, during the 1994–95 wheat-growing season. The experimental site lies at 25°38′N latitude and 88°41′E longitude at an altitude of 38 m. The soil is a sandy loam with a low pH (5.7) and below-critical levels of organic matter, nitrogen and boron (Saifuzzaman, unpublished data).

The three-factor factorial experiment was arranged in a split-plot design and replicated four times. Plot size was 3 m × 3 m. Seed was sown by hand in rows 20 cm apart.

Main plots received B at 0 or 1 kg/ha as borax (11% B). The sowing times were 20 November, 5 December and 20 December 1994. This increased the chances of crops being exposed to varying environmental growing conditions. Previous data and observations had indicated that foggy weather (high humidity) with low temperatures at some critical growth stage disposes wheat to sterility (Saifuzzaman, unpublished data). Three wheat genotypes were used in the subplots, representing varying degrees of susceptibility to boron deficiency and associated sterility: Fang 60 (low susceptibility), Kanchan (medium susceptibility) and SW 41 (high susceptibility).

The seed was treated with Vitavax™ 200 and sown at the rate of 120 kg/ha. N, P, K, S and Zn fertilizers were applied as urea (120 kg/ha), triple superphosphate (60 kg/ha), potassium chloride (40 kg/ha), gypsum (20 kg/ha) and zinc oxide (4 kg/ha). The urea was applied as two-thirds basal and one-third top-dressed at growth stage 20 of Zadoks et al. (1974). One irrigation was given immediately after sowing for better plant emergence. Three further irrigations were applied at stages 20, 50 and 70 of Zadoks et al. The site was weeded manually at 25 days after sowing.

Twenty to thirty flag leaves and young spikes were collected randomly, dried at 80°C for 72 hours and then shipped to Chiang Mai, where they were analysed for boron content following standard methods (AOAC 1984).

Results and Discussion

Phenology

The phenology of three wheat varieties in terms of days to flag leaf minus 1 (FL–1), booting, heading, anthesis and physiological maturity was recorded. There were highly significant interactions between seeding date and genotype on days to booting, heading and anthesis. Data indicated that growing environments, especially high temperature in the case of late-sown wheat, contributed to the differences. Only in the case of days to booting did boron levels and genotypes show a significant interaction. Other than this, no effect of boron or interaction between the factors was observed.

Sterility

Counts were made of all competent florets and all grains in each spike, and percentage sterility was calculated as 100 – (grains / competent florets × 100). Only genotypes showed highly significant differences in sterility between treatments (Fig. 1). The average sterility across all treatments was lower in Fang 60 (23.4%) than in Kanchan (30.3%) and SW 41 (28.7%). Lower sterility in Fang 60 could be due to its ability to produce higher numbers of grains per spike (56.4) or per spikelet (2.93), or could be associated with tolerance to sterility or low soil boron. There was no significant influence of any of the factors or interaction of the factors upon the grain set index (that is, fertility of the two lowest florets) from the 5th to the 14th spikelet of 10 central spikelets).

Rerkasem (1993) previously identified SW 41 as susceptible, Kanchan as intermediate, and Fang 60 as tolerant of boron deficiency as assessed by preventing sterility. This clear ranking did not apply in the present study (Fig. 1). In Bangladesh, Kanchan is cultivated on about 87% of wheat land (Meisner 1992). Since the 1986–87 growing season, severe sterility has been observed in Kanchan in some years but not in other years (Saifuzzaman 1994). In the 1994–95 wheat-growing season, humidity, light, temperature and rainfall in the north-western part of Bangladesh during the important critical growth stages were not so adverse as in earlier years. Sterility did not occur this year in this experiment and was minimal in growers' wheat fields in sterility-prone areas.

Boron concentration in flag leaf and young spike at booting

Boron concentrations in flag leaves at booting were significantly different between the three seeding dates (Fig. 2). Boron concentrations in the young spikes at booting were significantly different between the three genotypes. The critical boron concentrations below which severe grain set failure can occur are considered to be 4 to 7 ppm in flag leaves at the booting stage and 2 ppm in young spikes at booting (Rerkasem and Lordkaew 1992). In the zero boron treatment of this experiment, boron concentrations were at the critical level in the flag leaves (5.56 ppm) but above in the young spikes (4.97 ppm) averaged across all varieties. There was a high correlation between soil application of boron and boron concentrations in the flag leaves (r = 0.937) but not in young spikes. In previous work, tissue boron concentrations in flag leaves at booting also increased with increasing rates of soil application of boron, but there was no effect on sterility of wheat, regardless of whether the boron concentrations in the flag leaves were below or above the supposed critical level (Saifuzzaman, unpublished).

Yield and factors contributing to yield

Seeding dates and genotypes produced significant differences in grain yield (Fig. 3). The highest grain yield came from wheat sown on 5 December and there were highly significant interactions between seeding dates and genotypes. The highest grain yield came from Kanchan (5265 kg/ha) followed by Fang 60 (5203 kg/ha). Kanchan had a significantly higher thousand grain weight (44.7 g), though its grain number per spike (42.7) was lower than Fang 60's (56.4). Thousand grain weight was significantly lowest in Fang 60 (36.1), perhaps owing to a higher grain number. Though the grain size was lowest in Fang 60, it still yielded the same as Kanchan because of its higher grain number per spike. Grains per spikelet was highly significantly affected by genotypes and seeding dates (Fig. 4). Grains per spikelet could be used as a parameter to measure the extent of sterility in wheat because of its positive correlation with genotype (r = 0.82; p = 0.01) and negative correlation with sterility percentage (r = –0.73; p = 0.01).

Highly significant effects of seeding dates and genotypes, and sometimes the interactions, were evident in other parameters contributing to yield, such as grains per spike and spikes/m^2. However, no influence of boron or interactions with other factors were observed except the significant

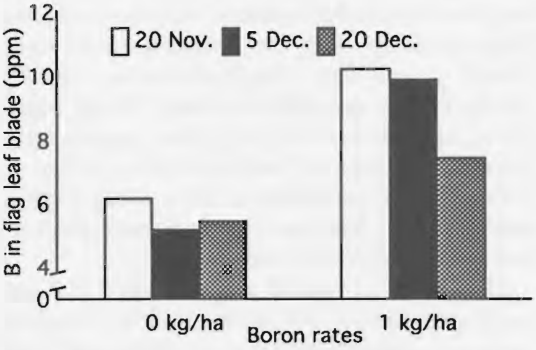

Figure 2. Effect of soil application of boron on the concentration of boron in the flag leaves at booting stage averaged over three genotypes (Wheat Research Centre, Dinajpur, 1994–95)

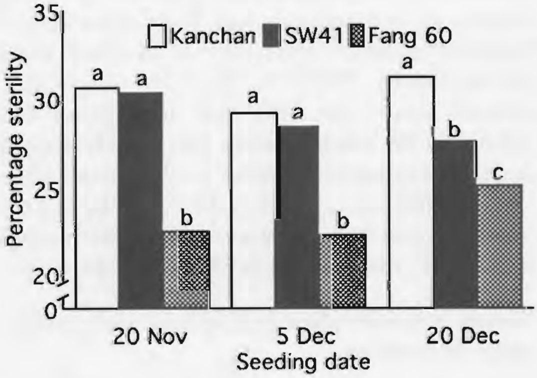

Figure 1. Effects of genotypes and seeding dates on percentage sterility (Wheat Research Centre, Dinajpur, 1994–95)

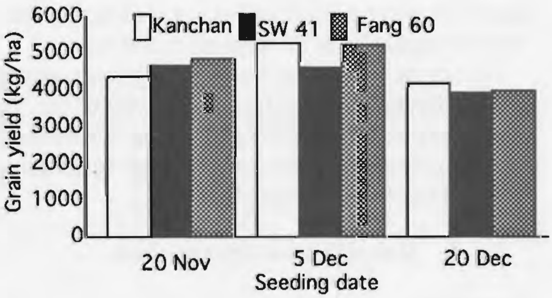

Figure 3. Effect of seeding dates and genotypes on wheat grain yield averaged over two boron levels (Wheat Research Centre, Dinajpur, 1994–95)

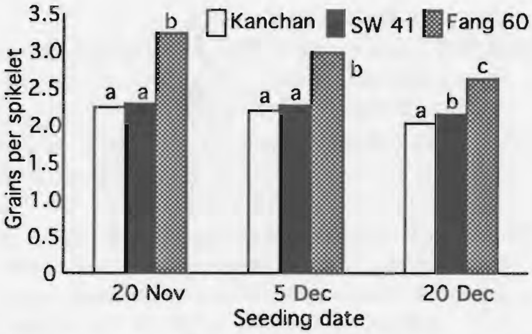

Figure 4. Effect of seeding dates and genotypes on the number of grains per spikelet averaged over two boron levels (Wheat Research Centre, Dinajpur, 1994–95)

interactions of boron and genotype on spikelets per spike. The differences between seeding dates and genotypes are due mainly to temperature. High temperature reduced the grain-filling period by about 13 days in the crop sown on 20 December compared with the crop sown on 20 November.

Conclusion

From the results, it can be concluded that there are genotypic differences in sterility under certain environmental conditions. Though boron has been shown to play an important role in causing or controlling the sterility of wheat in other Southeast Asian countries, in Bangladesh it is not the sole factor. Boron applications to the soil increased the boron concentration in the plant, but this increase did not affect sterility. Careful laboratory and field research programs are needed to address this complex problem of sterility.

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Effect of Sowing Time and Boron on Sterility in Four Genotypes of Wheat (*Triticum aestivum* L.) in the Western Hills of Nepal

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Abstract

This study determined the effect of sowing time and boron application on sterility in four genotypes of wheat (*Triticum aestivum* L.), SW 41, BL-1022, Fang 60 and BL-1249. The crops were planted on 21 November, 6 December and 21 December 1994, with or without boron applied at 1 kg/ha, at Rishing Patan, Nepal (420 m above sea level).

The effect of sowing time was significant for phenology, yield components, sterility and grain yield. Sterility was significantly increased in the crop planted on 21 December, which had the lowest grain yield. There was a significant genotypic difference for all the phenological variables measured, yield components, grain yield and sterility percentage. SW 41 and BL1022 had significantly higher sterility than the other genotypes. By contrast, Fang 60 had the lowest grain yield as a result of its lowest 1000-grain weight. BL-1249 had consistently lower sterility percentage over all sowing times and both boron rates.

Added boron had a significant effect on number of grains per spike, sterility percentage, 1000-seed weight and boron content in the flag leaf at anthesis. It had no effect on grain yield, but there were significant interactions between boron and genotype for the number of grains per spike and sterility percentage. This was because the two varieties susceptible to boron deficiency (SW 41 and BL-1022) responded to added boron, whereas the other two did not. Boron content in the flag leaf at anthesis increased with added boron in the soil but there was no significant genotypic difference for boron uptake. This indicates that some genotypes can set more grains than others with the same available boron.

WHEAT (*Triticum aestivum* L.) is the third most important cereal crop in Nepal after rice and maize in both area (620 000 ha) and production (873 000 t). Wheat is a winter crop and is cultivated from the *terai* (100 m) to high hills (2300 m). More than 80% of wheat cultivation is under the rice–wheat system (Hobbs 1990) and the remainder is under maize/finger-millet–wheat or maize–wheat or potato–wheat systems in upland areas.

The area and production of wheat increased sharply from the late 1960s with the introduction of Mexican varieties such as Lerma-52, Lerma Rojo-64 and the CIMMYT-bred Indian variety Sonalika (RR-21), combined with the use of chemical fertilizers and increased irrigation. From 1970 to 1990, the wheat area in Nepal increased by almost 100% and productivity increased by about 25%. However, while wheat has become an increasingly important crop, sterility (that is, grain set failure) has become an increasingly important problem.

Wheat sterility is widespread in subtropical rice–wheat systems of Asia. Problem areas identified include Nepal, Bangladesh, Thailand, Yunnan Province in China, Bihar and West Bengal in India, and Nepal (Mann and Rerkasem 1992). The causes of sterility are, however, different. In Nepal, this problem is increasingly becoming a serious constraint in both the rice–wheat system and maize-based farming. Under severe conditions, yield losses have been as high as 98% (Subedi et al. 1993). Wheat sterility can be caused by many environmental factors in various combinations. Boron (B) deficiency has been well established as a cause of wheat sterility (Singh et al. 1976; Li et al. 1978; Rerkasem et al. 1989; Sthapit 1988; Sthapit et al. 1989; Subedi et al. 1993). Genetic variability has been found for susceptibility to low boron (Mandal and Das 1988; Sthapit et al. 1989; Subedi et al. 1993; Rerkasem 1993). The seasonal and within-plot variability of sterility shows that boron availability must also be affected by other external factors.

When viewed externally, florets in sterile spikes appear to be complete with fully developed palea

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and lemma, but anthers are absent or are poorly developed and have a few malformed pollen grains (Rerkasem et al. 1989). When sterility is induced by boron deficiency or by other soil problems, the spikes appear transparent and patches of sterile crop can readily be identified. This is not the case when sterility is induced by cold. Then the problem occurs uniformly throughout the crop and spikes and peduncles turn black at maturity. Sterile spikes induced by cold remain green for much longer before they turn black, and sterile plants have more late tillers and spikes and the flag leaves remain green for longer than fertile plants (Subedi et al. 1993). In both types of sterility, the sterile spikes or patches of sterile plants can be distinguished from a distance.

This study reports the effects of boron and sowing time on sterility in four wheat genotypes. This is a joint experiment planned at the workshop 'Identification of causes of wheat sterility in subtropical Asia' held at Chiang Mai, Thailand, from 25 to 29 July 1994. The experiment was carried out by Lumle Agricultural Research Centre, Nepal.

Materials and Methods

Experimental site

The experiment was carried out at Rishing Patan (420 m altitude) in a rice–wheat rotation, where the problem of sterility in wheat has been high in previous years.

Design and treatments

The experiment was designed in a 3 × 4 × 2 factorial randomised complete block design with four replications. The factors were three sowing dates (21 November, 6 December and 21 December 1994), four genotypes (SW 41, BL-1022, Fang 60 and BL-1249) and two levels of boron (0 and 1 kg/ha). Of the four genotypes, SW 41 and BL-1022 had been identified as susceptible to boron deficiency, whereas Fang 60 and BL-1249 were known to be tolerant. Borax ($Na_2B_4O_7 \cdot 10H_2O$, 11% boron) was applied at 9 kg/ha (8 g borax per plot).

The gross experimental plot size was 3 m × 3 m and the net size was 2 m × 3 m. Seeds were sown continuously in small furrows 25 cm apart. The fertilizers used were urea (46% N), triple superphosphate (21% P), and potassium chloride (52% K). No organic manures were used. Half the nitrogen and all the phosphorus and potassium were applied in furrows before the wheat was sown. The remaining nitrogen was topdressed 30 days after sowing.

Soil information

Soil samples from the experimental site were taken from three depths (0–15 cm, 15–30 cm and 30–45 cm) and analysed. Results are shown in Table 1.

Meteorological records

Daily minimum and maximum temperatures and solar radiation (MJ/m²/d) were recorded at the experimental site. Additionally, temperature and relative humidity (RH) were recorded daily at 9 a.m. by a humidity and temperature meter (Vaisala HM 34). The readings of temperature, RH and radiation during the experimental period are presented in Table 2.

Field observations

After emergence (20 days after sowing), 20 random plants were marked in each plot and days to emergence of the 4th, 6th, 8th and flag leaves and beginning and completion of anthesis were recorded for the marked plants. Total crop duration—sowing to crop maturity—was also recorded. For boron analysis, blades of flag leaves and ears at flag leaf ligule emergence and anthesis were sampled from the 20 marked plants and dried for 48 hours at 70°C.

For the assessment of sterility, bulk samples of ears from a 1 m × 1 m area were taken at maturity and then 10% of these were taken as subsamples. From the subsamples the following observations were made:

a. No. of competent florets per spike
b. No. of grains per spike
c. No. of grains per $F_1 + F_2$ florets of 10 central spikelets (F_1 and F_2 are the first and second basal florets).

The sterility percentage was calculated from the above values by two methods:

1. Sterility (%) = (a – b) / a × 100
LAC method (Sthapit 1988).
2. Sterility (%) = (20 – c) / 20 × 100
CMU method (Rerkasem et al. 1989).

Grain yields were recorded from the sample taken from the 1 m² area and values were adjusted as 12% moisture. The data were statistically analysed.

Table 1.. Soil characteristics at the Rishing Patan site

Soil depth	Soil texture	pH	Total N%	Available P (ppm)	Exchangeable K meq/100 g soil	Boron (mg/kg)
0–15 cm	Silt loam	7.0 ± 0.20	0.19 ± 0.06	17 ± 1.3	0.18 ± 0.04	0.21 ± 0.18
15–30 cm	Silt loam	7.3 ± 0.14	0.06 ± 0.04	16.7 ± 1.20	0.09 ± 0.01	0.12 ± 0.03
30–45 cm	Silt loam	7.6 ± 0.0	0.08 ± 0.03	16.0 ± 5.0	0.08 ± 0.03	0.12 ± 0.01

Table 2. Mean minimum and maximum temperatures, relative humidity, maximum vapour pressure deficits (VPD) and solar radiation at the experimental site from the first sowing date to the final harvest (mean of 10 days)

Date 1994–95	°C min.	°C max.	°C at 9 a.m.	RH % at 9 a.m.	VPD max. (mb)	Radiation (MJ/m^2/d)
Sowing dates: 21 Nov., 6 Dec., 21 Dec.						
21 Nov. – 30 Nov.	11.7	25.3	16.5	78.6	17.5	–
1 Dec. – 10 Dec.	12.2	23.2	16.0	79.9	13.9	–
11 Dec. – 20 Dec.	9.6	22.9	14.1	79.5	15.1	–
21 Dec. – 30 Dec.	8.2	22.8	12.4	79.5	16.3	–
31 Dec. – 9 Jan.	5.8	21.4	10.8	81.4	14.9	–
10 Jan. – 19 Jan.	8.2	21.0	12.3	81.2	13.3	–
20 Jan. – 29 Jan.	8.1	20.4	19.9	81.4	5.1	10.8
30 Jan. – 8 Feb.	9.4	22.8	13.1	81.2	15.5	9.2
9 Feb. – 18 Feb.	10.7	23.4	14.6	79.7	15.5	10.3
19 Feb. – 28 Feb.	9.5	23.8	14.0	78.7	16.9	12.9
1 Mar. – 10 Mar.	11.6	26.4	16.2	79.6	19.8	14.5
11 Mar. – 20 Mar.	13.6	28.7	18.6	72.8	23.8	18.3
21 Mar. – 30 Mar.	17.4	31.7	22.4	74.3	26.6	16.8
31 Mar. – 9 Apr.	16.4	33.1	21.3	56.3	36.3	18.3
10 Apr. – 19 Apr.	18.5	33.7	22.7	63.4	34.8	18.4

Results and Discussion

The levels of significance (P) for different factors and their interactions for various measured variables are presented in Table 3.

Effect on phenology

The phenological variables recorded were days to emergence of the 4th, 6th, 8th and flag leaves, beginning of anthesis, completion of anthesis and days to maturity. The effect of various factors on the emergence of the 4th, 6th, 8th and flag leaves are presented in Table 4.

Effect of sowing date was significant for the emergence of the 4th, 6th, 8th and flag leaves. The crop sown on the third date (21 December) took longest to produce these leaves, followed by the second and first crops. This is mainly because of cool temperatures after the third sowing, which resulted in slow seedling emergence and slow subsequent development. It can also be seen from the temperature record (Table 2) that for the first sowing the mean minimum temperature within 10 days of crop sowing was 11.7°C, which reduced to 8.2°C for the third sowing; temperature continued to drop for at least one further month after the third planting date.

Added boron affected the emergence date of the 4th leaf only, delaying its appearance by one day

(29 v. 28 days). The reason for this is not known. There were no significant interactions between sowing date and boron for any phenological variable.

The effect of genotype was also significant for the emergence of the 4th, 6th, 8th and flag leaves. Fang 60 took significantly longer for the emergence of these leaves than the other three genotypes, which were similar to each other. No interactions were observed between genotype and boron or between genotype and sowing date (Table 4).

Boron had no effect on the timing of the beginning or completion of anthesis. There were highly significant interactions, however, between sowing time and genotype for the beginning of anthesis. Unlike leaf emergence, anthesis began sooner in the crop sown on 21 December than in the crops sown earlier (80 days v. 84 and 85 days) (Table 5). Fang 60 took significantly longer (88 days) to reach anthesis than the other varieties. BL-1249 was the earliest variety, with anthesis starting only 79 days after sowing.

The interaction between sowing date and genotype arose because SW 41, Fang 60 and BL1249 were significantly earlier at the third date than the first.

Similar results were also observed for the days to the completion of anthesis (Table 6). There was no effect of boron, nor were there interactions between boron and genotype or between boron and sowing date. The effect of sowing date arose because the crop sown on the third date (21 December) completed anthesis in 86 days after sowing, compared with 92 days for the second date and 94 days for the first date, which were not significantly different. Anthesis lasted 10 days in the first sown crop, 7 days in the second and 6

Table 3: Levels of significance (P) for different factors imposed on various variables measured

Variables	Genotypes (G)	Sowing date (D)	G× D	Boron (B)	G× B	D × B
Days to 4th leaf	<0.0001	<0.0001	>0.50	0.0047	>0.50	>0.50
Days to 6th leaf	<0.0001	<0.0001	0.256	>0.50	>0.50	>0.50
Days to 8th leaf	<0.0001	<0.0001	0.001	0.144	>0.50	0.372
Days to flag leaf	<0.0001	<0.0001	0.0001	>0.50	>0.50	>0.50
Days to anthesis start	<0.0001	<0.0001	0.0001	>0.50	>0.50	>0.50
Days to anthesis end	<0.0001	<0.0001	0.0002	0.241	>0.50	>0.50
Days to maturity	<0.0001	>0.50	>0.50	>0.50	>0.50	>0.50
Spikelets per spike	<0.0001	0.100	0.069	>0.50	0.051	>0.50
Florets per spike	<0.0001	<0.0001	0.026	0.063	0.073	>0.50
Grains per spike	<0.0001	>0.50	0.023	0.0007	0.0008	>0.50
1000 grain weight	<0.0001	<0.0001	0.077	0.029	0.350	>0.50
Sterility (LAC method)	<0.0001	<0.0001	0.258	0.0001	0.0002	0.096
Sterility (CMU method)	<0.0001	0.106	>0.50	0.008	0.004	>0.50
Grain yield	0.0002	<0.0001	0.053	0.115	>0.50	>0.50
Boron content in flag leaf (at FLLV*)	0.186	>0.50	>0.50	>0.50	>0.50	>0.50
Boron content in ear (at FLLV*)	0.152	>0.50	>0.50	>0.50	>0.50	0.016
Boron content in flag leaf (at anthesis)	0.160	0.367	>0.50	0.010	>0.50	0.234
Boron content in ear (at anthesis)	>0.50	>0.50	>0.50	>0.50	0.211	0.184

* FLLV = flag leaf ligule visible

Table 4. Effect of sowing time and boron on the phenology of different genotypes of wheat at Rishing Patan, 1995 (B = boron, D = sowing date, G = genotype)

	Days to emergence of											
	4th leaf			6th leaf			8th leaf			Flag leaf		
	B–	B+	Mean	B–	B+	Mean	B–	B+	Mean	B–	B+	Mean
Sowing date												
21 November	25	25	25	39	39	39	64	65	65	64	65	65
6 December	28	29	28	45	45	45	64	65	65	65	65	65
21 December	31	32	31	46	46	46	67	67	67	67	67	67
Mean	28	29	28	43	44	44	65	66	66	65	66	67
SED (B)		0.31***			0.42 ns			0.45 ns			0.45 ns	
SED (D)		0.38***			0.51***			0.55***			0.55***	
SED (B × D)		0.54 ns			0.72 ns			0.78 ns			0.78 ns	
Genotype												
SW 41	27	28	28	44	44	44	65	65	65	65	65	65
BL-1022	27	28	27	42	43	43	64	64	64	64	65	64
Fang 60	29	31	30	45	45	45	68	70	69	68	69	69
BL-1249	28	28	28	42	42	42	64	64	64	64	65	64
Mean	28	29	28	43	44	44	65	66	66	65	66	66
SED (G)		0.44***			0.58***			0.65***			0.64***	
SED (B × G)		0.63 ns			0.83 ns			0.92 ns			0.90 ns	

*** = highly significant at the P < 0.001 level

days in the third. This difference was due solely to changing temperatures. Thermal time summations above a base of 0°C were respectively 160°Cd, 129°Cd and 128°Cd. The base temperature for the heading to anthesis period is approximately 9°C (Slafer and Rawson 1995). Night temperatures fell below this base during anthesis for the first sowing study, so actual thermal sums would in reality have been lower than 160°Cd.

Fang 60 took the longest time from sowing to completion of anthesis (95 days), followed by SW 41 (92 days), BL-1022 (89 days) and BL-1249 (87 days). There was no difference, however, between the four genotypes for the period between beginning and completion of anthesis (Tables 5 and 6).

There was also a genotype × sowing time interaction for the completion of anthesis. Rising temperatures shortened the period of anthesis for the last-sown crop.

The number of days to maturity was influenced only by sowing date. There was no effect of boron or genotype or of any interactions between the factors. The crop sown on 21 December matured in 112 days compared with 125 days for the 6 December crop and 129 days for the 21 November crop. The 21 December crop faced higher temperatures; its reproductive period, as a proportion of its total crop duration, was reduced.

Effect on yield components

Number of spikelets per spike

The number of spikelets per spike was influenced by genotype but not by the sowing date or boron rate. Fang 60 had the most spikelets (17.0 per spike) followed by SW 41 (15.7 per spike), BL-1022 (15.5 per spike), and BL-1249 (14.6 per spike). There was a significant genotype × boron interaction for this component. This was because added boron increased the number of spikelets in SW 41 but reduced it in BL-1249 (Table 7).

Table 5. **Effect of sowing date and genotype on days to the beginning of anthesis of wheat averaged over two boron rates at Rishing Patan, 1995**

Genotype	Sowing date			Mean across dates
	21 Nov.	6 Dec.	21 Dec.	
SW 41	87	86	81	85
BL-1022	80	83	79	80
Fang 60	91	90	84	88
BL-1249	79	79	77	79
Mean across genotypes	84	85	80	83

SED genotypes (G) = 0.55***, SED sowing date (D) = 0.51***, SED (G × D) = 1.01***
*** = highly significant at the $P < 0.001$ level

Table 6. Effect of sowing time and genotype on the days to completion of anthesis of wheat averaged over two boron rates at Rishing Patan, 1995

Genotype	Sowing date			Mean across dates
	21 Nov.	6 Dec.	21 Dec.	
SW 41	97	94	87	92
BL-1022	89	91	87	89
Fang 60	100	97	89	95
BL-1249	89	88	83	87
Mean across genotypes	94	92	86	91

SED genotypes (G) = 0.70***, SED sowing date (D) = 0.60***, SED(G × D) = 1.21***
*** = highly significant at the $P < 0.001$ level

Number of florets per spike

The number of florets per spike was influenced by sowing date and genotype (Table 8). Number of florets was significantly less in the 6 December crop (46.3 per spike) than in the crops sown on 21 December (51.9 per spike) and 21 November (50.2 per spike). Fang 60 had the largest number of florets (53.8 per spike), followed by BL-1022 (49.9 per spike). BL-1249 (47.3 per spike) and SW 41 (47.0 per spike) had significantly fewer than the other two genotypes.

There was also a significant interaction between genotype and sowing date for the number of florets per spike. This was because Fang 60 had similar floret numbers from all sowing dates, whereas BL-1022 had significantly fewer (44.2 per spike) from the second sowing date.

No effect of boron or of its interactions with sowing date and genotype was observed.

Number of grains per spike

The number of grains per spike was influenced by genotype and boron but not by sowing date. Number of grains was highest in Fang 60 (43.2 per spike) and lowest in SW 41 (33.3 per spike).

Application of boron at 1 kg/ha increased the number of grains set from 37.2 to 40.4 per spike. There was also a highly significant interaction between genotype and boron level (Table 9). This arose because grain set increased significantly in SW 41 (from 29.8 to 36.9 per spike) and in BL-1022 (from 35.9 to 42.6 per spike) with the application of boron.

Effect on 1000-seed weight

All factors had an effect on 1000-seed weight: sowing date, genotype and boron. There were no interactions, however, between any of the three factors. The effects of sowing time and genotype are shown in Table 10.

The 1000-seed weight was significantly reduced when sowing was delayed after 21 November, from 44.5 g in the 21 November crop to 40.2 g in the 6 December crop and 32.1 g in the 21 December crop. Factors that would have reduced grain weight included increased temperatures during the reproductive period (Table 2), which reduced the grain-filling period from 35 days to 33 and 26 days, respectively, and reduced moisture in the soil associated with increasing vapour pressure deficits (these increased from 21.8 mb to 28.3 and 31.7 mb respectively for the average of the grain-filling period).

There was also a genotypic difference for seed weight. Fang 60 had a significantly lower seed weight (28.2 g/1000 seed), though it had a higher number of grains per spike. This is presumably because it reached anthesis last, giving it a longer period to produce a high floret number, but giving it the least time to complete the grain-filling period because of increasing temperatures and VPDs.

Application of boron at 1 kg/ha increased grain set per spike in the boron responsive genotypes, but it reduced overall grain weight significantly (40.0 g cf. 37.9 g/1000 seed).

Effect on sterility

Sterility percentage was estimated by two methods. The results followed a similar pattern except that there was no effect of sowing date on sterility percentage estimated by the CMU method. The LAC method estimated about 13.5% higher sterility (21.7% v. 8.2%). The results presented here are based on the LAC method.

Sterility percentage was influenced by all three factors imposed (Table 11). Irrespective of genotype and boron, sterility was higher in the late-sown crop (25.8%) than in the first-sown crop (21.5%). The second crop had the lowest sterility (17.9%) (Table 11). Among the four genotypes, SW 41 had the highest sterility (29.3%), followed by BL-1022 (21.5%), Fang 60 (19.6%) and BL-1249 (16.6%). BL-1249 had previously been reported to be tolerant to boron deficiency (Subedi et al. 1993). No interaction was observed between sowing date and genotype.

Application of boron at 1 kg/ha significantly reduced the overall sterility from 24.0% to 19.5%, but did not remove it completely. There was a strong interaction, however, between genotype and boron. In the boron-susceptible genotypes, sterility reduced from 34.4% to 24.2% in SW 41 and from 25.8% to 17.2% in BL-1022. In the other genotypes there was no positive response to added boron; indeed, sterility was significantly lower when boron was not added (Fig. 1).

Table 7. Effect of sowing date and genotype on the number of spikelets per spike of wheat averaged over three planting dates at Rishing Patan, 1995

Genotype	Boron rate		Mean across boron rates
	B–	B+	
SW 41	14.4	16.0	15.7
BL-1022	15.5	15.5	15.5
Fang 60	17.3	16.7	17.0
BL-1249	15.6	14.7	14.6
Mean across genotypes	15.7	15.7	15.7

SED genotypes (G) = 0.33***, SED boron (B) = 0.16 ns, SED (G × B) = 0.33*
*** = highly significant at the $P < 0.001$ level
* = highly significant at the $P < 0.05$ level

Table 8. Effect of sowing time and genotype on the number of florets per spike of wheat averaged over two boron rates at Rishing Patan, 1995

Genotype	Sowing date			Mean across dates
	21 Nov.	6 Dec.	21 Dec.	
SW 41	46.8	44.2	48.5	47.0
BL-1022	51.3	44.2	54.1	49.9
Fang 60	54.4	52.6	54.3	53.8
BL-1249	46.0	44.8	50.6	47.3
Mean across genotypes	50.2	46.3	51.9	49.5

SED genotypes (G) = 1.00***, SED sowing date (D) = 0.87***, SED (G × D) = 1.75*
*** = highly significant at the $P < 0.001$ level
* = highly significant at the $P < 0.05$ level

Table 9. Effect of genotype and boron on the number of grains per spike of wheat grouped under boron responsive and boron non-responsive genotypes at Rishing Patan, 1995

Genotype	Boron rate		Increase (+) or decrease (–) in grains set per spike
	B–	B+	
Boron responsive genotypes			
SW 41	29.8	36.9	+7.1
BL-1022	35.9	42.6	+6.7
Boron non-responsive genotypes			
Fang 60	44.2	42.3	–1.9
BL-1249	39.0	39.8	+0.8
Mean across all genotypes	37.2	40.4	+3.2

SED genotypes (G) = 1.25***, SED boron (B) = 0.88***, SED (G × B) = 1.77***
*** = highly significant at the $P < 0.001$ level

Table 10. Effect of sowing time and genotypes on the 1000-seed weight (g) of wheat averaged over two boron rates at Rishing Patan, 1995

Genotype	Sowing date			Mean across dates
	21 Nov.	6 Dec.	21 Dec.	
SW 41	50.5	40.4	31.9	40.9
BL-1022	47.4	43.8	36.4	42.5
Fang 60	32.6	30.0	22.0	28.2
BL-1249	47.5	46.7	38.2	44.2
Mean across genotypes	44.5	40.2	32.1	38.9

SED genotypes (G) = 1.38***, SED sowing date (D) = 1.20***, SED (G × D) = 2.39 ns
*** = highly significant at the $P < 0.001$ level

Table 11. Effect of sowing time and genotype on sterility percentage (LAC method) of wheat averaged across two boron rates at Rishing Patan, 1995

Genotype	Sowing date			Mean across dates
	21 Nov.	6 Dec.	21 Dec.	
SW 41	28.0	26.7	33.2	29.3
BL-1022	20.5	17.8	26.1	21.5
Fang 60	18.5	14.5	25.9	19.6
BL-1249	19.1	12.8	17.8	16.6
Mean across genotypes	21.5	17.9	25.8	21.7

SED genotypes (G) = 1.48***, SED sowing date (D) = 1.29***, SED (G × D) = 2.59 ns
*** = highly significant at the $P < 0.001$ level

The higher sterility in the 21 December sown crop might have arisen because of drought. There was not enough water to irrigate the crop, with the result that there was moisture stress during the latter part of flowering.

The other climatic factors, such as temperature, relative humidity at 9 a.m. and solar radiation, were unlikely to have caused sterility as they were not extreme. For example, the crop sown on 21 November started anthesis 84 days after sowing (Table 5) and completed it 94 days after sowing (Table 6). This period falls between 13 and 23 February, when mean minimum temperature was 10°C, RH was 79% and solar radiation was 12 MJ/m^2/d. In comparison, the last-sown crop completed its anthesis between 11 and 20 March, when mean minimum and maximum temperatures were 13.6°C and 28.7°C, RH at 9 a.m. was 72.8% and solar radiation was high, 18.3 MJ/m^2/d. However, maximum vapour pressure deficits (VPD) during these periods did increase from 15.5 mb to 23.8 mb. These differences would have resulted in the late-sown crop transpiring some 35% faster than the first crop during anthesis. This would have exacerbated the moisture stress problem, and could have contributed to sterility.

Effect on boron uptake

The surface soil boron content of the experimental site was 0.21 ± 0.08 ppm (Table 1), which is sufficiently low to cause sterility. Plant uptake of boron was analysed. Boron content in the flag leaf and ears at flag leaf ligule visible (FLLV) and anthesis was analysed. This showed that there was no significant difference in boron content in either flag leaf or ears at FLLV stage, but that there was a significant effect of boron treatment on the flag leaf boron content at anthesis (Table 12). Boron content of the flag leaf was higher than in the ear. There was no significant difference in genotype or sowing date for the uptake of boron in all cases.

That there was no effect of genotype on flag leaf boron content implies that genotypes take up similar amounts of boron but that they have different abilities to tolerate boron deficiency and to set grains with the amount of boron available. In this case, BL-1249 and Fang 60 set more grains than other genotypes, even though they had a similar concentration of boron in their flag leaves.

Effect on grain yield

There were significant effects of sowing date and genotype on grain yield (adjusted to 12% moisture), but no effects of boron. The crop sown on 21 November produced the highest grain yield (4.16 t/ha), which was significantly higher than that from the 6 December crop (3.63 t/ha). The late-sown crop produced the lowest yield (2.74 t/ha).

There was also a great genotypic difference in grain yield. Irrespective of sowing date, Fang 60 produced the lowest grain yield (1.70 t/ha),

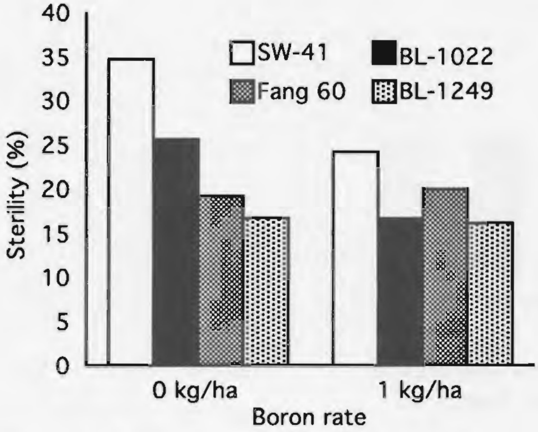

Figure 1. Effect of genotype and boron on wheat sterility percentage averaged across three sowing dates at Rishing Patan, 1995

primarily because it had the lowest 1000-seed weight.

There was also a genotype × sowing time interaction, which is shown in Figure 2. The interaction arose because of the significantly lower grain yield of SW 41 at the third sowing date. This was not the case in the first two sowing dates, when SW 41 produced significantly higher yields than Fang 60. The grain yield of BL-1249 was relatively consistent across sowing dates, suggesting that it performs better under stressed or late-sown conditions. The lower grain yield of SW 41 at the third date was due to increased sterility (29.3%).

Conclusion

This experiment clearly demonstrated genotypic differences in sterility. SW 41 and BL-1022 were sensitive to boron deficiency but Fang 60 and BL-1249 were tolerant. Similarly, there was also a marked effect of sowing time on sterility, grain yield and other variables measured. Sterility was more related to soil problems than to the weather at Rishing Patan. The higher sterility in the late-sown crop was presumed to be caused primarily by limiting soil moisture and higher vapour pressure deficits during anthesis, though the reduced grain-filling period linked with higher temperature might have contributed.

There was a clear indication that added boron can reduce sterility. However, the degree of reduction in sterility percentage associated with boron applications was not very high, and some sterility remained. There were no differences between genotypes in tissue boron content for a given level of boron application, but some varieties set more grains for a specific boron content than others. Boron content in the flag leaf was more than in the ear.

In terms of grain yield, sterility and other related variables, the right time to sow wheat in this region appears to be around 21 November. If sowing is delayed until 6 December, almost a 50% yield reduction results. The effect of moisture stress on boron uptake is one area of research associated with this problem.

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Table 12. Boron content (mg/kg) in the flag leaf and ear of wheat at Rishing Patan, 1995, averaged across three sowing dates and four genotypes

Stage	Plant part	B–	B+	Mean	SED
Flag leaf ligule visible	Flag leaf	3.51	3.41	3.46	0.22 ns
	Ears	3.22	3.33	3.27	0.11 ns
Anthesis	Flag leaf	4.18	4.57	4.38	0.15**
	Ears	3.24	3.06	3.18	0.18 ns

** = significant at the $P < 0.01$ level; ns = not significant

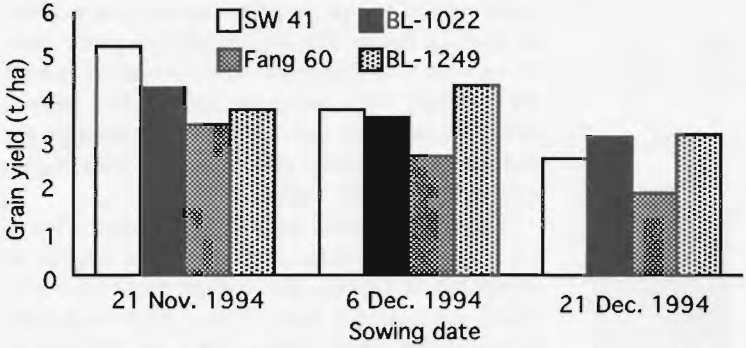

Figure 2. Effect of genotype and sowing time on the grain yield (t/ha) of wheat averaged over two boron rates at Rishing Patan, 1995

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Effects of Sowing Time and Boron on Sterility in Wheat in Dehong Prefecture, China

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Abstract

A wheat sterility experiment was conducted in Dehong Prefecture, China, with three varieties, three planting dates and two boron treatments. Data on weather, soil, plant and boron content that were thought to be related to wheat sterility were collected. It appears that there are differences between varieties in sensitivity to boron deficiency: sensitive varieties are poorer at extracting boron from the soil. For these varieties, lower available boron and earlier planting date can increase sterility.

DEHONG Prefecture lies in the south-west of Yunnan Province, China. No wheat was planted there before 1957. In the late 1970s, sterility became one of the main barriers to wheat production. In 1984, no wheat was harvested on more than 40 hectares of farmland. During and following this extreme year, researchers began a series of investigations. They found that genotype, planting date, soil water capacity, temperature, dry hot winds and boron limitation, singly and in combination, could cause wheat sterility (Zhang 1984, Zhen 1984, Li 1988). Measures that were taken to overcome the problems have had some success, but the problem still exists in some locations, especially in sandy soils with low inputs. The purpose of the current experiment was to study the effects of planting date and boron on wheat sterility.

Methods

The experiment was planted at the Dehong Prefecture Agricultural Research Institute (latitude 24°04′N, longitude 98°01′E, altitude 913 m). Following the design agreed to with ACIAR, there were 72 plots each 2 m × 4.5 m, three varieties (SW 41, Fang 60 and Yun-38), three planting dates (26 October, 10 November and 25 November 1994), two boron treatments (nil and 10 kg/ha borax) and four replications. (Yun-38 is a Yunnan Academy of Agricultural Sciences (YAAS) variety.)

Superphosphate at 750 kg/ha and urea at 168 kg/ha were applied as basal fertilizers. A further equivalent dose of urea was applied at tillering. Field operations included irrigation at emergence, tillering and stem elongation, one spray of insecticide to control aphids, and one spray of herbicide for weed control. Data collection included weather data; soil characteristics including available boron; plant phenological development; boron content in the plant ears and leaves; and seed set and yield. Hot-water-soluble boron in the soil was analysed before sowing and after harvest by the Soil Research Institute of YAAS, and in the ear and flag leaf samples by Chiang Mai University.

Results and Discussion

Soil profile and boron content

The soil is mainly a loam with three horizons: the cultivation layer (0–18 cm), the plough pan or under-plough layer (18–28 cm) and the heart soil layer (> 28 cm). The cultivation layer is a yellow-brown loam with a pH of 6.5. The plough pan layer is a deep brown light clay with a pH of 6.0. The heart soil layer has a pH of 7.2. The water table is 110 cm below the surface. Available boron (hot-water-soluble) before sowing was only 0.12 ppm, much lower than the accepted critical value in China of 0.5 ppm, so the soil was boron-deficient. Unfortunately, because superphosphate with a boron concentration of 81 ppm (approximately equivalent to 0.6 kg/ha of borax (Dr B. Rerkasem, pers. comm.)) was applied to the plots, the soil was contaminated. Variability of sterility in farmers' fields could be associated with the use of superphosphate that contains boron.

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Phenology of the three varieties from different planting dates

From Table 1 it can be seen that, although there was almost one month's range in sowing dates, there was only about 10 days' difference in flowering dates.

Effects of planting date on yield and sterility

Results in Table 2 show that although there was no difference in grains per spike between planting dates in each variety, yield was significantly affected by planting date. Later planting resulted in lower yield because in Dehong, planting too late exposes plants to frequent high temperatures and hot dry winds during grain-filling. This results in premature maturity and an obvious decrease in 1000-grain weight.

There was some effect of planting date on sterility in SW 41—the earlier the planting, the higher the sterility—but little effect in Fang 60 and Yun-38 (Table 2). The different responses by genotypes are possibly related to varietal sensitivity to boron deficiency. Differences cannot be explained by differing environmental conditions during the development and formation of pollen grains because the genotypes had similar flowering dates (Table 1). The difference in performance is likely to be because SW 41 is a susceptible variety whereas Fang 60 and Yun-38 are tolerant or resistant to low boron.

One explanation for the difference in sterility index in SW 41 between the three planting dates (Table 2) is that the gradual increase in evaporation with later planting resulted in more boron uptake from the soil (Fig. 1). Another is that the low night temperatures, averaging 3.5°C between 20 and 31 January, increased pollination failure in the crops that were sown first. Between 1 and 10 February, when plants from later sowings were flowering, the average minimum night temperature was 6.5°C. Further experimentation is required to confirm these suggestions.

Effect of boron treatment on sterility

From Table 2 it can be seen that there was no significant effect of boron treatment on sterility index, yield and grains per spike in the three varieties, possibly because the soil had been contaminated by the use of superphosphate that contained boron. However, the difference in the sterility index of SW 41 between the B0 and B+ treatments is comparatively higher than that of the other two varieties, though it does not reach significance.

Effects of planting dates and boron treatment on boron in the ear and flag leaf

In general, boron concentrations in the flag leaf increased with later planting date (Table 3), which accords with the trend of pan evaporation (Fig. 1).

Compared with the B0 treatment, applying borax increased boron concentration in both ear and flag leaf, especially the latter, and the concentrations in the flag leaf were significantly higher than in the ear. This could imply that one of the important roles of boron in the wheat plant

Table 1. Timing of growth stages of wheat sown at three sowing dates in Dehong Prefecture

Variety	Date sown	Date emerged (E)	Date flowered (F)	Date mature (M)	E–F days	F–M days	E–M days
SW 41	26 Oct	2 Nov	28 Jan	5 Apr	87	67	154
	10 Nov	20 Nov	3 Feb	8 Apr	75	64	139
	25 Nov	2 Dec	8 Feb	12 Apr	68	63	131
Fang 60	26 Oct	2 Nov	28 Jan	5 Apr	87	67	154
	10 Nov	20 Nov	3 Feb	8 Apr	75	64	139
	25 Nov	2 Dec	8 Feb	12 Apr	68	63	131
Yun-38	26 Oct	2 Nov	2 Feb	31 Mar	92	57	149
	10 Nov	20 Nov	5 Feb	6 Apr	77	60	137
	25 Nov	2 Dec	8 Feb	8 Apr	68	59	127

Table 2: Yield components of crops grown with no boron (B0) and 10 kg borax per ha (B+)

Genotype	Date sown	Sterility index*		Yield (t/ha)		Grains per spikelet	
		B0	B+	B0	B+	B0	B+
SW 41	26 Oct	8.73	6.57	2612	2652	44.2	45.9
	10 Nov	4.26	3.07	2102	2253	45.9	46.3
	25 Nov	3.41	3.41	1721	1676	40.4	42.1
Fang 60	26 Oct	1.39	1.80	2527	2598	49.7	52.7
	10 Nov	1.46	1.19	2199	2303	54.1	52.0
	25 Nov	1.82	0.61	1820	1776	50.5	49.6
Yun-38	26 Oct	3.29	2.98	2530	2658	64.2	64.5
	10 Nov	1.93	2.57	2585	2208	68.5	65.3
	25 Nov	1.55	2.48	1980	2174	56.2	54.0

$$* \text{ Sterility index} = \frac{\text{sterile basal florets of 10 middle spikelets}}{\text{20 basal florets of 10 middle spikelets}} \times 100$$

is to help photosynthesis and the transport of photosynthate, as in rape (Lu and Shenkang 1990).

There is a varietal difference in ability to take up boron. For the ear, it is Fang 60 > Yun-38 > SW 41. For the flag leaf, it is Yun-38 > Fang 60 > SW 41. Overall, therefore, SW 41 has the lowest boron uptake into the ear and flag leaf.

Conclusions

Because the experiment in Dehong was conducted during only one season, the results might not be representative of long-term trends. However, we can still draw three conclusions:

- For SW 41, planting dates and boron treatments have some effect on sterility, but they do not reach significance in this study. The degree of sterility was minimal in all treatments (< 9%).
- Compared with the low-boron-tolerant varieties Fang 60 and Yun-38, the susceptible variety SW 41 has a lower capacity to extract boron from the soil, at least during the period when the ear and flag leaf are developing.
- For all varieties and planting dates, the boron concentration in the flag leaf is clearly higher than that in the ear. Besides affecting fertility, boron is therefore also very important for leaf function.

Acknowledgments

We are grateful to Dr Benjavan Rerkasem for boron analysis of the ears, flag leaves and fertilizers, and also thank Dr Howard Rawson for providing the devices for measuring radiation, temperature and humidity, and for helpful advice.

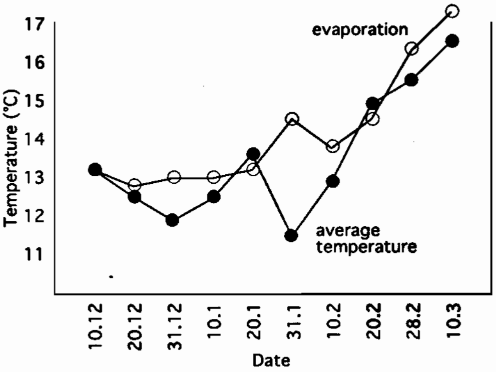

Figure 1. Average temperature (°C) and pan evaporation (mm) during the main growing stages of wheat from 10 December 1994 to 10 March 1995

Table 3. Boron concentration of ear and flag leaf from different planting dates and boron treatments. Samples taken at flag leaf ligule emergence (FLLE) and anthesis (samples analysed by Dr B. Rerkasem)

		Boron in ear (ppm)				Boron in flag leaf (ppm)				Boron in ear + flag leaf			
		FLLE		Anthesis		FLLE		Anthesis		FLLE		Anthesis	
Variety	Date sown	B0	B+	B0	B+	B0	B+	B0	B+	B0	B+	B0	B+
SW 41	26 Oct	3.26	3.10	2.96	3.09	3.60	3.83	3.49	4.03	6.86	6.93	6.45	7.12
	10 Nov	3.15	3.63	3.32	3.55	3.74	4.57	3.85	4.40	6.89	8.20	7.17	7.95
	25 Nov	3.28	3.58	2.93	3.24	4.27	4.92	3.35	4.68	7.55	8.50	6.28	7.92
Fang 60	26 Oct	4.44	3.88	4.46	4.96	4.91	5.21	4.66	4.32	9.35	9.09	9.12	9.28
	10 Nov	4.30	4.47	4.87	4.93	5.25	5.81	4.51	5.16	9.55	10.3	9.38	10.1
	25 Nov	4.07	4.51	4.31	4.98	6.40	7.32	4.99	7.05	10.5	11.8	9.30	12.0
Yun-38	26 Oct	3.60	3.78	3.81	4.51	5.95	6.22	5.86	6.04	9.55	10.0	9.67	10.6
	10 Nov	3.56	4.50	3.41	4.08	6.14	6.29	5.32	7.01	9.70	10.8	8.73	11.1
	25 Nov	3.96	3.87	3.47	3.03	7.07	6.35	6.89	7.13	11.0	10.2	10.4	10.2
	Mean	3.74	3.92	3.73	4.04	5.26	5.61	4.77	5.54	8.99	9.54	8.50	9.58

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Effects of Boron, Planting Date and Genotype on Sterility in Wheat in Thailand

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Abstract

This experiment evaluated responses, measured primarily as percentage sterility, of several wheat genotypes at three locations in the Chiang Mai area to boron (B) application (B0 and B+) and three sowing dates. The effect of B was by far the largest on grain set. By contrast, the effect of sowing date was not significant ($P < 0.05$) at any location. Genotypic variation in response to boron confirmed patterns in the literature. Grain set in Fang 60 was less severely affected by B deficiency in B0, and responded less to B application, than SW 41 and B1022. An effect of planting date on responses to B of genotypes was small and evident only in the pot sand culture, where the difference between B0 and B+ was large and B deficiency in B0 was extreme.

Materials and Methods

The experiment was conducted at three sites:

- Chiang Mai University (CMU) in Chiang Mai (18°47′N 98°9′E, 314 m a.s.l.), in pot sand culture (Rerkasem and Loneragan 1994), with nine genotypes, designated CMU-sand. The sand is a siliceous quartz with virtually no trace of B that could be detected with hot water extraction (hot-water-soluble B, or HWSB).
- In the field at the Multiple Cropping Centre's Irrigated Agriculture Station in Chiang Mai, with nine genotypes, designated CMU-field. The soil is a sandy loam (Tropaqualf) of the San Sai series, with a HWSB concentration of 0.15 mg/kg.
- In the field at the Samoeng Upland Rice and Temperate Cereals Station, 40 km from Chiang Mai (820 m), with four genotypes, designated Samoeng. The soil is a relatively heavier reddish clay loam, with a HWSB concentration of 0.16 mg/kg.

The wheat genotypes are listed in Table A.

Two rates of boron were used at each site. In the CMU-sand experiment these were 0 and 1 µM B applied twice daily with all other essential nutrients (B0 and B+). In the field experiments they were 0 and 1 kg/ha as borax (B0 and B+).

The three sowing dates (D1 to D3) are shown in Table B. There were four replications in each experiment.

Table A. Wheat genotypes sown at CMU and Samoeng

Genotype	Source	Location used
SW 41	Thailand	CMU and Samoeng
Fang 60	Thailand	CMU and Samoeng
BL-1022	Nepal	CMU and Samoeng
SMGBW 88001	Thailand	CMU and Samoeng
BL-1249	Nepal	CMU
Kalyasona	Bangladesh	CMU
Kanchan	Bangladesh	CMU
M283	Pakistan	CMU
Soghat 60	Pakistan	CMU

Maximum and minimum temperatures and pan evaporation for the period of the study at Chiang Mai and Samoeng are shown in Table C.

Chiang Mai was some 4°C hotter during the day and 1.5°C hotter at night than Samoeng and tended to have lower pan evaporation late in the season.

Fertility of ears was gauged by use of the grain set index (GSI). This is the percentage of the two basal florets of each of the 10 central spikelets that contain a grain (Rerkasem and Loneragan 1994).

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Table B. Sowing dates used at CMU and Samoeng

	CMU-sand	CMU-field*	Samoeng
D1	19.11.94	18.11.94	27.11.94
D2	30.11.94	13.12.94	08.12.94
D3	14.12.94	28.12.94	21.12.94

* The two CMU experiments were planned for similar planting dates, but rain delayed the second planting in the field, which then delayed the third planting.

Table 1. Effects of boron and planting date (D1 to D3) on grain set index (GSI %) in nine wheat genotypes in sand culture

Sown	19.11 (D1)		30.11 (D2)		14.12 (D3)	
Genotype	B0	B+	B0	B+	B0	B+
SW 41	0	70.6	0	82.9	2.5	85.4
Fang 60	73.5	98.2	25.4	96.2	61.8	97.9
BL-1022	0	82.8	0	90.5	0	82.4
SMGBW 88001	1.2	93.1	0	88.8	0	83.6
BL-1249	0	81.9	1.2	77.9	2.2	84.5
Kalyasona	5.1	85.4	0	96.2	8.5	95.2
Kanchan	0	85.2	1.5	92.2	4.8	92.9
M283	0	86.0	5.0	94.5	0	88.4
Soghat 60	4.8	78.1	1.5	89.8	6.8	96.2
Mean	9.4	84.6	3.8	89.9	10.8	89.6

SE1 (G***, G × B***, G × D***, B × D × G*) = 5.9
SE2 (B***, B × D***) = 6.7 SE3 (D ns) = 8.1
G = genotype, B = boron, D = date
ns = not significant ($P < 0.05$), * = significant at $P < 0.05$, *** = significant at $P < 0.001$

Results and Discussion

CMU-sand

Grain set data in this experiment were obtained from ears that were bagged as they were emerging to prevent cross-pollination.

Without added B in the nutrient solution, eight of the nine genotypes set almost no grain (Table 1). Fang 60, with a GSI in B0 of 25.4% to 73.5%, was the exception. Adding B increased GSI to more than 70% in all genotypes.

Statistics indicated clear interactions between B and planting date, to which genotypes responded differently. For seven of the nine genotypes (SW 41, BL-1022, SMGBW88001, BL-1249, Kanchan, M283 and Soghat 60), there was virtually no grain set in B0 for all three planting dates. For two of these seven genotypes, there was a slight depression in grain set in B+ in SW 41 and Soghat 60 for the first planting date, but not in the other five.

Although the effect of planting date on the sterility response to B was statistically significant, it must be noted that the main effect of B on sterility was generally much greater.

The response to planting date in Fang 60 with added B, which had a significant depression in grain set for the second planting date, deserves further examination.

Table C. Maximum and minimum temperatures and pan evaporation for the period of the study

	Chiang Mai				Samoeng			
	Max. °C	Min. °C	Mean °C	Evap. mm/day	Max. °C	Min. °C	Mean °C	Evap. mm/day
Nov. 94	31.2	17.6	24.4	3.6	26.2	15.4	20.8	3.1
Dec. 94	29.6	16.4	23.0	3.0	25.6	14.9	20.3	3.2
Jan. 95	31.0	14.7	22.9	3.4	27.2	14.1	20.7	3.8
Feb. 95	32.5	14.8	23.7	3.3	29.0	14.3	21.7	5.6
Mar. 95	36.7	20.1	28.4	4.3	32.7	17.6	25.2	6.5
Mean	32.2	16.7	24.5	3.5	28.1	15.3	21.7	4.4

CMU-field

Grain set

There was a statistically significant, but minor, effect of B in which GSI tended to increase with B application (Table 2). Grain set depression in the absence of B was seen in SW 41, BL-1022, SMGBW88001 and M283. No effect of planting date was detected, either as a main effect or in interaction with B.

Grain yield

Few treatment effects were detected in grain yields (Table 3). Stand establishment was poor in a number of replicates in several treatments, so grain yield was not statistically analysed.

Tissue boron

Only the B0 samples were analysed as all of the B+ samples were lost in a fire in the oven. There were no significant differences (Tables 5 and 6). Without boron application, the concentrations of boron in the flag leaf (4–5 mg/kg dry weight) and ear (3–4 mg/kg dry weight) at boot stage were in the range previously found to be associated with deficiency and grain set failure (Rerkasem and Lordkaew 1992; Rerkasem and Loneragan 1994).

Table 2. Effects of boron and planting dates on grain set index (GSI %) in nine wheat genotypes in the field at CMU

Sown	18.11 (D1)		13.12 (D2)		28.12 (D3)	
Genotype	B0	B+	B0	B+	B0	B+
SW 41	78.2	89.5	88.5	91.2	86.2	92.0
Fang 60	91.8	96.5	93.5	96.0	84.5	88.8
BL-1022	89.8	95.2	80.5	97.0	96.5	96.5
SMGBW 88001	94.8	96.2	87.0	98.5	96.5	96.2
BL-1249	89.0	92.2	86.8	94.2	90.0	93.0
Kalyasona	94.5	95.8	92.2	90.8	94.5	93.5
Kanchan	91.2	92.0	89.8	91.0	92.2	94.5
M283	85.8	94.0	82.8	94.8	93.8	96.0
Soghat 60	91.5	91.0	91.5	87.5	92.2	90.2
Mean	89.6	93.6	88.1	93.4	91.8	93.4

SE1 (G***, G × B***, G × D*, B × D × G ns) = 3.9
SE2 (B***, B × D ns) = 4.6 SE3 (D ns) = 2.9

Table 3. Effects of boron and planting date on grain yield in nine wheat genotypes in the field at CMU

Sown	18.11 (D1)		13.12 (D2)		28.12 (D3)	
Genotype	B0	B+	B0	B+	B0	B+
SW 41	231	267	148	250	112	117
Fang 60	203	212	237	nd	100	134
BL-1022	199	248	202	283	178	159
SMGBW 88001	304	303	187	213	219	213
BL-1249	201	191	281	230	156	193
Kalyasona	229	278	201	197	116	102
Kanchan	264	248	234	191	102	131
M283	296	258	244	242	53	178
Soghat 60	160	216	131	nd	96	90
Mean	232	247	207	229	137	146

nd = not determined, establishment poor in all replicates

Grain size (1000-grain weight)

Table 4. Effects of boron and planting date on 1000-grain weight (g) in nine wheat genotypes in the field at CMU

Sown	18.11 (D1)		13.12 (D2)		28.12 (D3)	
Genotype	B0	B+	B0	B+	B0	B+
SW 41	39.1	35.4	30.6	26.0	19.1	18.4
Fang 60	27.3	28.6	23.0	25.6	18.5	16.3
BL-1022	38.8	35.1	32.2	32.1	30.2	27.8
SMGBW 88001	37.5	36.8	38.4	35.7	30.8	30.6
BL-1249	38.3	38.1	36.9	33.2	29.6	31.6
Kalyasona	31.5	32.1	25.1	23.6	17.9	17.9
Kanchan	37.4	35.9	32.8	31.5	19.9	24.0
M283	39.0	34.8	33.1	29.8	23.2	25.7
Soghat 60	25.5	27.5	21.0	22.6	17.0	15.3
Mean	34.9	33.8	30.3	28.9	22.9	23.1

SE1 (G***, G × B ns, G × D***, B × D × G*†) = 2.1
SE2 (B**, B × D ns) = 2.5 SE3 (D***) = 2.7
*† = significant at $P < 0.1$, ** = significant at $P < 0.01$

Samoeng

Grain set

At Samoeng, there was a significant effect of B × G on GSI. Fang 60, as previously, exhibited no sign of B deficiency in B0, and did not respond to B application (Table 7). SW 41, BL1022 and, to a lesser extent, SMGBW88001 were clearly depressed by B deficiency. Sowing date had no effect on GSI, nor did it influence response of the genotypes to B.

Grain yield

Grain yield data (Table 8) were much more variable than GSI (Table 7). The main effect of B was significant, but G × B was not ($P < 0.05$). Late sowing tended generally to lower the grain yield, though there were some genotypic differences. However, there was no evidence that sowing date influenced the effect of B on grain yield.

Grain size (1000-grain weight)

B deficiency also had a general effect of increasing grain size (Table 9).

Tissue boron

Boron application had a general effect of increasing B concentration slightly in the flag leaf at boot stage, but not in the ear (Table 10). Even in the flag leaf, however, no relationship was found between the B concentration and grain set in Table 7. As at Chiang Mai, tissue B concentrations at Samoeng were also in the deficient range. The slight effect of B application on tissue B should also serve as a reminder of the difficulty associated with trace element trials in the field. Lack of response to boron application has often been observed in the field. Before an interpretation that boron is not a limiting factor can be made, however, the effectiveness of applied B should be first ascertained.

Table 5. Effects of planting date on boron (mg/kg dry weight) in the flag leaf and ear of nine wheat genotypes in the B0 treatment at boot stage in the field at CMU

Sown	16.11 (D1)		13.12 (D2)		28.12 (D3)	
Genotype	Flag	Ear	Flag	Ear	Flag	Ear
SW 41	4.1	2.5	5.0	4.0	3.8	2.6
Fang 60	4.4	2.9	5.0	5.2	4.5	3.0
BL-1022	4.5	2.5	5.2	3.7	3.8	2.6
SMGBW 88001	4.6	2.5	5.7	3.7	3.9	3.7
BL-1249	5.2	3.4	5.3	4.3	3.6	5.9
Kalyasona	3.9	2.8	4.4	4.1	3.5	2.8
Kanchan	4.2	2.7	4.8	4.0	4.3	2.3
M283	2.8	2.1	5.2	3.7	3.5	2.7
Soghat 60	4.1	1.9	5.6	4.4	3.7	2.7
Mean	4.2	2.6	5.1	4.1	3.8	3.1

Table 6. Effects of planting date on boron (mg/kg dry weight) in the flag leaf and ear of nine wheat genotypes in the B0 treatment at anthesis in the field at CMU

Sown	16.11 (D1)		13.12 (D2)		28.12 (D3)	
Genotype	Flag	Ear	Flag	Ear	Flag	Ear
SW-41	5.5	3.4	6.1	3.4	8.0	4.9
Fang 60	6.1	3.7	6.8	4.5	9.3	5.3
BL-1022	5.8	2.9	6.8	3.3	8.0	4.9
SMGBW 88001	5.7	2.9	7.1	3.7	10.1	4.6
BL-1249	5.6	3.5	6.5	4.0	10.0	5.2
Kalyasona	6.4	3.1	6.9	4.0	8.2	4.9
Kanchan	5.2	3.5	7.0	4.0	8.8	4.7
M283	6.1	2.6	7.2	3.4	8.4	4.7
Soghat 60	6.5	2.9	10.0	4.1	8.6	4.8
Mean	5.9	3.2	7.2	3.8	8.8	4.9

Table 7. Effects of boron and planting date on grain set index (GSI %) in four wheat genotypes in the field at Samoeng

Sown	27.11 (D1)		8.12 (D2)		21.12 (D3)	
Genotype	B0	B+	B0	B+	B0	B+
SW 41	83.5	88.0	47.0	70.8	43.2	77.8
Fang 60	98.8	98.2	99.5	99.5	85.0	94.5
BL-1022	73.2	75.5	34.0	89.5	73.5	96.0
SMGBW 88001	96.0	90.8	85.0	94.0	75.5	98.5
Mean	87.9	88.1	66.4	88.5	69.3	91.7

SE1 (G***, G × B*, G × D*, B × D × G ns) = 10.8
SE2 (B**, B × D ns) = 13.4
SE3 (D ns) = 10.3

Table 8. Effects of boron and planting date on grain yield (kg/ha) in four wheat genotypes in the field at Samoeng

Sown	27.11 (D1)		8.12 (D2)		21.12 (D3)	
Genotype	B0	B+	B0	B+	B0	B+
SW 41	1995	2058	1300	1694	1404	1784
Fang 60	2063	2138	2044	2129	1538	1737
BL-1022	1994	2077	1306	2010	1584	1953
SMGBW 88001	1699	1812	1964	2180	1404	1784
Mean	1938	2021	1653	2003	1482	1814

SE1 (G ns, G × B ns, G × D***, B × D × G ns) = 210
SE2 (B*, B × D ns) = 299 SE3 (D*) = 283

Table 9. Effects of boron and planting date on 1000 grain weight (g) in four wheat genotypes in the field at Samoeng

Sown	27.11 (D1)		8.12 (D2)		21.12 (D3)	
Genotype	B0	B+	B0	B+	B0	B+
SW 41	45.8	44.5	42.5	41.8	36.2	34.5
Fang 60	39.5	38.5	37.5	36.2	35.0	34.5
BL-1022	48.2	43.5	48.0	46.8	42.5	40.2
SMGBW 88001	43.8	45.2	44.8	46.0	42.0	44.0
Mean	44.3	42.9	43.2	42.7	38.9	38.3

SE1 (G**8, G × B*†, G × D*, B × D × G ns) = 2.2
SE2 (B*, B × D ns) = 2.2
SE3 (D*) = 3.4
*† = significant at P < 0.1

Comparing variance ratios (*f* values) of various factors and their interactions across experimental sites

The main effect of B was by far the largest affecting grain set, particularly in sand culture (Table 11). In contrast, effect of sowing date on GSI was not significant ($P < 0.05$) at all three locations. Effect of planting date on responses to B of genotypes was evident only in the sand culture; that is, when the difference between B0 and B+ was large, or in other words, B deficiency in B0 was extreme.

Conclusions

This experiment has clearly shown that boron deficiency is the primary factor causing sterility in wheat in this environment. The range of environmental conditions as affected by sowing date or altitude (Chiang Mai at 314 m and Samoeng at 820 m) had only slight effect on sterility or its response to boron. This was true when boron deficiency was severe (in sand culture) or moderate (in the field at CMU and Samoeng).

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Table 10. Effects of boron and planting date on boron concentration (mg/kg dry weight) in the flag leaf and ear at boot stage of four wheat genotypes in the field at Samoeng

Sown	27.11 (D1)		8.12 (D2)		21.12 (D3)	
Genotype	B0	B+	B0	B+	B0	B+
Flag leaf						
SW 41	3.4	4.1	2.5	3.5	3.2	4.1
Fang 60	3.7	3.6	3.2	4.1	4.9	4.7
BL-1022	3.0	3.9	3.2	3.4	3.8	3.9
SMGBW 88001	3.6	4.6	3.4	4.2	3.6	4.4

SE1 (G*, G × B ns , G × D ns, B × D × G ns) = 0.5
SE2 (B***, B × D ns) = 0.3
SE3 (D*) = 0.4

Ear						
SW 41	2.8	2.2	2.8	2.6	2.7	3.1
Fang 60	3.5	3.0	3.2	3.6	3.3	3.3
BL-1022	2.6	2.9	2.6	2.5	2.8	2.7
SMGBW 88001	3.4	3.8	3.8	3.1	3.3	3.6

SE1 (G**, G × B ns, G × D ns, B × D × G ns) = 0.4
SE2 (B ns, B × D ns) = 0.4
SE3 (D ns) = 0.5

Table 11. Variance ratios (*f* values) of effects of various factors and their interactions on GSI (%) across three experiments

Effect	Variance ratios (*f* values)		
	CMU-sand culture	CMU field	Samoeng field
Boron (B)	3844 ***	16.77***	14.88**
Date (D)	0.004 ns	3.868 ns	4.447 ns
Genotype (G)	39.42***	3.242***	17.57***
B × G	17.18***	2.306***	3.032*
B × D	7.75***	1.549 ns	3.595 ns
D × G	3.823***	1.953*	3.199*
B × G × D	1.722*	1.098 ns	1.545 ns

Floret Sterility and Grain Yield of Bread Wheat Cultivars under Different Environments

Khushnood A. Siddiqui*

Abstract

Four bread wheat varieties, Fang 60, SW 41, Soghat 90 and S-175, were planted on three sowing dates, 13 November, 30 November and 17 December 1994, at Tandojam. The different sowing dates exposed the crops to different environments. Temperatures ranged from a minimum of 6°C to a maximum of 42°C. Yields varied between 3.9 and 6.7 t/ha. Sterility varied between 12% and 30%, but floret sterility was not correlated with sowing date or with yield. The highest values of sterility occurred in S-175, where they were largely correlated with excessive spike length, excessive number of spikelets and number of florets per spike, particularly when planting was delayed.

PAKISTAN was the first developing country in Asia to achieve self-sufficiency in wheat production (Borlaug 1989). Wheat has remained the central theme of the self-sufficiency program in Pakistan. It claims three times the area and twice the value-added share of cotton and rice, which are Pakistan's two main export earners.

The research work at the Atomic Energy Agricultural Research Centre was begun in 1967 to solve the problems arising from the Green Revolution. Breeding for tolerance to drought, salt and high temperature and improving multiple cropping systems are some of the research objectives of this program. The main objective is the development of new, high-yielding, disease-resistant wheat varieties endowed with high protein content and high quality.

Development of new varieties is being achieved by exploiting useful interactions between genotype and environment to match the growth cycle with the growing environment. Removal of constraints, including the elimination of sterility, has been the central theme of this endeavour.

Boron deficiency is not a problem in Pakistan, but drought, soil salinity and high temperature induce significant sterility in wheat. Grain yield is greatly influenced by a wide variety of factors, including high temperature in this part of the world. It is ultimately determined by the efficiency of the second growth stage, from flower primordium initiation to anthesis (Bozzini 1986), as well as by the third stage, from anthesis to kernel ripening (Siddiqui 1982; Bozzini 1986). The second stage is very sensitive to adverse temperature, which severely affects the development of the male gametophyte, leading often to male sterility or to more or less complete sterility (Bozzini 1986; Siddiqui 1994).

The present experiment was designed during the last workshop held in Chiang Mai (Bell and Rerkasem 1994). This experiment is unusual as it does not take into consideration boron deficiency.

Materials and Methods

Four bread wheat varieties—Fang 60, SW 41, Soghat 90 and S-175—were planted at the Tandojam Research Centre on three sowing dates—13 November, 30 November and 17 December 1994, exposing the crops to three combinations of weather variables. The combinations are referred to here as environments. Each experiment was replicated in a randomised complete block design with a plot size of 3 m × 3 m. Maximum and minimum daily temperature and relative humidity were recorded in the field during the wheat-growing season. Observations of ear emergence, maturity, plant height, grain yield and components of grain yield were collected. Sterility percentage of florets was calculated. Data were statistically analysed and correlation coefficients were worked out to determine the meaningful relationships between floret sterility and grain yield and yield components.

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Results and Discussion

Weekly weather data from the experimental site are shown in Table 1. For the most part, temperatures remained favourable to the growth of the wheat crop. However, maximum temperatures were higher than 30°C in November and the first week of December, exceeded 35°C in the third week of March and reached 40°C in the second week of April (Table 1).

In the first environment, which had a minimum average temperature of 16.3°C and a maximum average of 33.4°C, Soghat 90 produced the significantly highest yield ($p < 0.05$) (Table 2). In the second environment, where minimum average temperatures ranged from 13°C to 24°C and maximum from 30°C to 34°C, S-175 was the highest-yielding cultivar and SW 41 produced the significantly lowest yield ($p < 0.05$). The third environment, characterised by high temperatures, reduced the grain-filling period and eliminated any significant grain yield differences between the cultivars (Table 2).

The phenological traits—days to ear emergence, days to maturity and duration of the grainfilling period—were also affected by the changing environments (Table 3). Differences between cultivars were also significant. S-175 required longer to reach ear emergence and maturity. The grain filling period of S-175 was shortened by high temperatures in April and May. Fang 60 took longest for grain filling in each environment (Table 2).

The cultivars were also evaluated for their plant architecture. Plant height and internode lengths were highest in the second environment (Table 4),

Table 1. Weather data from Tandojam during the experiment, 1994–95

Month	Week	Minimum °C		Maximum °C		Humidity %	
		Range	Mean	Range	Mean	Range	Mean
October	3	16–17	16.3	36–37	36.3	68–83	77.7
	4	17–21	19.6	33–36	34.8	75–100	85.6
November	1	16–18	17.2	34–36	35.0	76–86	80.5
	2	15–18	16.3	31–35	33.4	69–90	80.6
	3	13–17	16.0	30–33	31.3	80–90	82.7
	4	13–24	15.3	30–34	31.3	80–100	88.7
December	1	15–17	16.4	30–32	30.8	82–91	88.8
	2	06–17	9.1	22–31	25.0	53–87	76.8
	3	09–12	10.5	25–29	26.5	71–87	78.1
	4	07–12	10.0	20–28	23.7	56–94	80.3
January	1	08–11	9.8	22–24	23.0	59–88	78.6
	2	06–09	8.0	20–24	21.1	59–94	87.6
	3	06–10	7.8	19–25	22.0	51–94	82.7
	4	10–13	11.6	24–28	25.9	57–890	74.3
February	1	12–13	12.4	25–28	26.4	59–81	68.9
	2	09–15	12.2	24–32	28.5	53–81	75.0
	3	08–12	10.2	25–29	27.0	67–100	78.0
	4	09–10	9.3	24–28	26.3	80–80	80.0
March	1	09–15	11.7	22–28	26.0	63–71	65.7
	2	10–18	12.8	27–33	29.6	40–72	71.2
	3	15–22	17.3	29–36	31.9	58–82	64.8
	4	14–17	15.3	34–38	35.5	59–67	64.8
April	1	14–20	16.6	34–42	37.4	34–69	51.8
	2	16–22	19.5	34–40	37.8	45–70	60.0
	3	18–23	20.5	32–38	35.8	72–84	78.0
	4	18–25	21.5	36–40	38.3	53–85	71.5

Table 2. Mean grain yield (kg/ha) of wheat cultivars under varying environments

Cultivars	Environments (sowing date)			
	13 November	30 November	17 December	Mean across environments
SW 41	6611 a*	4500 b	3944 a	5018
Fang 60	5778 b	5678 a	4125 a	5194
Soghat 90	6750 b	5403 a	3986 a	5389
S-175	4861 c	5695 a	4086 a	4481
Mean across cultivars	6000	5319	4035	

* Numbers with the same letter are not significantly different.

which could be regarded as the most suitable period for the vegetative growth of wheat. As ear emergence in S-175 was comparatively late, the plants of this cultivar were taller, with comparatively shorter first and second internodes, but a longer third internode.

The cultivars varied significantly for spike characters (Tables 5 and 6). S-175 had the longest spike length, with significantly more spikelets and florets per spike, and the greatest floret sterility percentage. There were no significant differences between cultivars for number of seeds or grain weight per spike.

Floret sterility was not significantly correlated with sowing date. Most of the correlation coefficients of floret sterility against yield components were non-significant. However, floret sterility established positive correlations with spike length, number of spikelets per spike and number of florets per spike when planting was delayed (Table 7).

Table 3. Phenological traits of wheat cultivars under varying environments

Cultivars	Environments (sowing date)			
	13 November	30 November	17 December	Mean across environments
Days to ear emergence				
SW 41	73 c	75 c	72 c	73.3
Fang 60	75 c	76 c	70 c	73.7
Soghat 90	80 b	82 b	78 b	80.0
S-175	95 a	95 a	90 a	93.3
Mean across cultivars	80.8	82.0	77.5	
Days to maturity				
SW 41	119 c	122 c	112 c	117.7
Fang 60	126 bc	128 b	120 b	124.7
Soghat 90	130 b	132 b	120 b	127.3
S-175	142 a	140 a	126 a	136.0
Mean across cultivars	129.3	130.5	119.5	
Grain filling period (days)				
SW 41	46	47	40	44.3
Fang 60	51	52	50	51.0
Soghat 90	50	50	42	47.3
S-175	47	45	36	42.7
Mean across cultivars	48.5	48.5	42.0	

Conclusions

This study has shown that some floret sterility can occur even in the high-yielding environments of Tandojam. Sterility did not differ between the low-boron-sensitive (SW 41) and low-boron-tolerant (Fang 60) genotypes, in keeping with the fact that boron is not a limiting factor at this site. Almost all the observed sterility was associated with large numbers of spikelets per spike, which occurred in one of the local genotypes, and the problem increased with delayed sowing.

The causes of sterility in Tandojam are unlikely to be the same as have been identified in other countries of the region, namely boron deficiency and low temperatures during heading and anthesis.

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Table 4. Plant architecture of different wheat cultivars under varying environments

Cultivars	Environments (sowing date)			
	13 November	30 November	17 December	Mean across environments
Plant height (mm)				
SW 41	843 b	943 b	857 b	881
Fang 60	845 b	1008 a	896 a	916
Soghat 90	868 b	952 b	895 ab	905
S-175	995 a	1025 a	931 a	984
Mean across cultivars	888	98.20	89.45	
First internode length (mm)				
SW 41	360 a	389 b	344 b	364
Fang 60	385 a	407 ab	367 a	386
Soghat 90	373 ab	419 a	385 a	392
S-175	335 c	356 c	333 b	341
Mean across cultivars	363	393	357	
Second internode length (mm)				
SW 41	179 a	198 b	185 b	187
Fang 60	168 a	230 a	201 a	200
Soghat 90	179 a	203 b	182 ab	188
S-175	185 a	172 c	182 b	180
Mean across cultivars	178	200	188	
Third internode length (mm)				
SW 41	96 b	113 b	99 bc	103
Fang 60	99 b	131 a	107 b	113
Soghat 90	101 b	111 b	98 c	104
S-175	126 a	130 a	128 a	128
Mean across cultivars	106	121	108	

Table 5. Spike characters of wheat cultivars under varying environments

Cultivars	Environments (sowing date)			
	13 November	30 November	17 December	Mean across environments
Spike length (mm)				
SW 41	113 b	116 a	105 b	111
Fang 60	121 b	143 a	107 b	124
Soghat 90	117 b	118 a	105 b	113
S-175	172 a	176 a	180 a	176
Mean across cultivars	136	138	124	
Spikelets per spike				
SW 41	19.7 c	22.4 b	20.5 b	20.7
Fang 60	20.1 c	21.5 c	20.1 b	20.6
Soghat 90	22.2 b	23.1 b	19.5 b	21.6
S-175	29.1 a	29.8 a	29.8 a	29.6
Mean across cultivars	22.8	24.2	22.44	
Florets per spike				
SW 41	63.2 a	71.2 a	65.5 b	66.6
Fang 60	62.3 a	69.0 a	63.2 b	64.8
Soghat 90	61.4 a	68.2 a	63.5 b	64.4
S-175	71.0 a	77.6 a	77.2 a	75.2
Mean across cultivars	64.4	71.5	67.3	

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Table 6. Spike characters of wheat cultivars under varying environments

Cultivars	Environments (sowing date)			
	13 November	30 November	17 December	Mean across environments
Floret sterility (%)				
SW 41	13.2 b	13.7 b	14.6 b	13.8
Fang 60	19.0 ab	14.6 b	12.4 b	15.3
Soghat 90	15.1 ab	14.6 b	16.2 b	15.3
S-175	20.0 a	19.8 a	29.9 a	23.2
Mean across cultivars	16.8	15.7	18.3	
Seeds per spike				
SW 41	54.7 a	61.3 a	55.8 a	57.3
Fang 60	50.6 a	59.0 a	55.5 a	55.0
Soghat 90	52.1 a	58.2 a	53.2 a	54.5
S-175	56.7 a	62.2 a	54.1 a	57.7
Mean across cultivars	53.6	60.2	54.6	
Grain yield per spike (g)				
SW 41	2.08 a	2.17 a	1.66 a	1.97
Fang 60	2.11 a	1.95 a	1.62 a	1.89
Soghat 90	1.97 a	1.84 a	1.54 a	1.78
S-175	2.10 a	2.02 a	1.59 a	1.90
Mean across cultivars	2.06	1.99	1.60	

Table 7. Correlation coefficients of floret sterility against yield and yield components under varying environments

Floret sterility (%) against	Environments (sowing date)		
	13 November	30 November	17 December
Florets per spike	0.120 ns	0.369 ns	0.738**
Spike length	0.459 ns	–0.285 ns	0.897**
Spikelets per spike	0.429 ns	0.629**	0.883**
Seeds per spike	–0.352 ns	–0.059 ns	–0.210 ns
Grain yield per spike	–0.487 ns	–0.374 ns	–0.221 ns

ns = not significant ($p > 0.05$), ** = significant at $p < 0.01$

Controlled environment research within the project

Effects of Temperature, Light and Humidity during the Phase Encompassing Pollen Meiosis on Floret Fertility in Wheat

H. M. Rawson*, M. Zajac* and R. Noppakoonwong*†

Abstract

This paper examines the effects of temperature, humidity and light, altered during the period surrounding pollen meiosis, on floret fertility of wheat. A companion paper in these Proceedings examines the effects of these environmental variables against a background of marginal and zero soil boron.

There were no significant differences between the two genotypes Fang 60 and SW 41 in their responses to a reduction of light from 950 to 500 μmol/m²/s during the phase from emergence of the second-last leaf ligule to early grain filling. Plant height was marginally increased under less light (2.2%), ear number was reduced (26%), and ears were shorter (6.7%) and had fewer florets (22%), which were less fertile (8.2%). The overall effect of reduced light was a 28% reduction in grain number.

The averaged effects of increasing mean temperature from 12° to 20°C during the phase were large. Plants were 16% shorter and produced 10% fewer ears, which were 8% shorter and had 9% fewer florets; these florets were 9% less fertile, leading to a 16% reduction in grain number per main ear.

By contrast with temperature, the averaged effects of reducing humidity from nominally 80% to 40% were very small and generally insignificant. However, responses to humidity interacted significantly with temperature and radiation. Thus, high humidity always reduced floret fertility (to 83.4% mean) regardless of temperature when light was low; that is, only 21.6 mol/m²/d, or equivalent to field conditions in spring. The reductions were greater at higher temperature (to 73.2% mean) in keeping with earlier findings. The most severe condition for sterility with adequate boron in the growth medium was high humidity combined with high temperature and low radiation. It is calculated that transpiration integrated over the pollen meiosis phase could be reduced by 88% by this combination of treatments compared with that in the contrasting environments.

It is concluded that environmental factors can change floret fertility in the presence of boron in the growth medium. This does not rule out boron limitation in the sexual growth centres as a cause, particularly as boron uptake is largely dependent on transpiration rate, which was changed by the environmental factors in this experiment.

DURING the past two decades, many cereal crops in the subtropics have been observed to be partially sterile (e.g. Singh et al. 1976; Ganguly 1979; Mandal 1994). Some observers have noted that sterility appears to be most severe when temperatures are high, humidities are low and there are hot winds (e.g. Galrao and Sousa 1988). In controlled environments also, high temperatures have been found to reduce grain set (Saini and Aspinall 1982a,b; Saini et al. 1983; Wardlaw 1994), though poorer grain set in those instances has occurred under high rather than low humidity (Bagga and Rawson 1977; Dawson and Wardlaw 1989; Tashiro and Wardlaw 1990). Water stress has been implicated (Saini and Aspinall 1981).

Evidence has accumulated that wheat genotypes can differ markedly in their degree of sterility in equivalent subtropical conditions (Singh et al. 1976; Ganguly 1979; Chatterjee et al. 1980; Rerkasem et al. 1993; Rerkasem and Loneragan 1994). In all these studies, the degree of sterility of the genotypes was linked with their differential requirement for boron when they were grown in severely boron-deficient soils. It is interesting, however, that the genotype Janak, which showed greatest sterility and greatest response to added boron in the field studies conducted between 1971 and 1977 (Ganguly 1979; Chatterjee et al. 1980), was also found to be sterile under high humidity in controlled environment work (Bagga and Rawson 1977). In the controlled environment studies, boron was added daily in a nutrient solution and so should not have been limiting.

There is little doubt that the most common direct cause of devastating sterility in the subtropics is a

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limitation of boron. In the cereals the sterility seems to show itself as poorly formed anthers or infertile pollen (Cheng and Rerkasem 1993). A clear sign of this is 'gaping glumes': the lemma and palea remain open after anthesis for several days instead of the normal several hours. This same visible response is also characteristic of sterility associated with high humidity. Limiting boron results in poor growth, sterility or both, not only in wheat, but also in a wide range of other species (Berger et al. 1957; Ifteni and Toma 1977; Garg et al. 1979; Mozafar 1987; Galrao and Sousa 1988). The effects can be reduced or avoided by the addition of boron either to the soil or as late foliar sprays (e.g. Chatterjee et al. 1980 in wheat). But even in these other species there is some evidence that factors such as radiation and temperature (Forno et al. 1979) can modify the responses to boron. The overall picture seems to be one in which sterility is often linked with limiting boron but the effects vary depending on environmental conditions.

It has been suggested that boron moves primarily in the transpiration stream (Kohl and Oertli 1961), though small amounts can move in the phloem (Shelp 1987). Consequently, it might be expected that any environmental factor that modifies transpiration rate might also modify the degree of sterility by altering the availability of boron to the sexual growth centres. By corollary, it might also be expected that sterility would vary from year to year in the field where factors affecting transpiration rate also vary, and that the variability would be greatest in areas where boron availability is marginal.

Vapour pressure deficit (VPD) is the environmental variable that has most influence on transpiration rate. In the absence of changes in stomatal aperture, transpiration rate increases linearly with VPD, the slope of the response varying with species (Rawson et al. 1977; Rawson and Clarke 1988). As VPD is determined by temperature and relative humidity, it would be expected that all these factors would modify the uptake of boron into the plant.

The aim of this paper and its companion paper (Rawson and Noppakoonwong, these Proceedings) is to examine the hypothesis that the degree of sterility in wheat is linked with boron availability in the growth medium and the ability of the plant to use that boron as influenced by transpiration rate and rate of growth. Transpiration rate was ostensibly modified by having two humidity treatments in combination with two temperature regimes (that is, four environment treatments). Rate of growth (that is, rate of demand) was ostensibly modified by changing temperature. Following Bingham (1966) and Saini and Aspinall (1981, 1982b), it was assumed that the critical phase leading to sterility in wheat is the period surrounding pollen meiosis (Bennet, Finch et al. 1973; Bennet, Rao et al. 1973), which is marked approximately by emergence of the flag leaf ligule (Dawson and Wardlaw 1989). The environment treatments were therefore applied only during the period encompassing that phase. Before the emergence of the second-last leaf ligule, all plants were grown in a single environment.

The first study, reported here, used a growth medium to which a complete nutrient solution was added daily to test whether the four environmental treatments would change fertility in the absence of a 'soil' boron limitation. Two genotypes were tested which contrasted in their responses to boron in earlier studies (Rerkasem and Loneragan 1994). The second study, which is the subject of the companion paper, added boron as a treatment as the two boron concentrations used were considered marginal, unlike in this first study.

Materials and Methods

Plants of two genotypes of wheat, Fang 60 and SW 41, both from Thailand, were grown in a glasshouse in the Canberra phytotron (Morse and Evans 1962). The glasshouse temperature was maintained between extremes of 27° and 13°C following a daily sine curve. Maximum temperature occurred at 1 p.m. The growth medium was a 50:50 mix of vermiculite and perlite in 100 × 150 mm pots (volume 1.18 L) to which was added a full Hoagland solution each morning and tap water each afternoon. Liquid was added until the pots dripped. There were 16 pots of each genotype in each treatment, split into four blocks.

The treatments of the two genotypes were two temperatures by two humidities by two light regimes. One set of plants remained in the initial glasshouse condition throughout. Treatments began when the ligule emerged on the leaf before the flag leaf. This leaf number was determined by dissection of some plants, which were then discarded. At that stage, plants were moved from the glasshouse to artificially lit growth cabinets maintained at 27°day / 13°C night (as in the glasshouse) or 17°/7°C sine curve. Both high and low temperature regimes were set for 80% and 40% relative humidity (four cabinets). Continuous monitoring showed that the set temperatures were achieved but the set humidities were not. In the high temperature treatment, actual mean daily relative humidities were 83.4 ± 0.11% and 49.9 ± 0.08% (vapour pressure deficits of 3.88 and 11.71 mb respectively), and in the low temperature treatment they were 84.4 ± 0.07% and 67.7 ± 1.33% (VPDs of 2.19 and 4.53 mb). The two light regimes were 950 and 500 μmol/m²/s maintained for 12 hours each day. The lower light regime was achieved by the use of frames covered with aluminium-stranded cloth over half the plants in each cabinet.

As each main ear emerged at least 50% above the flag leaf, and well before anthesis occurred, the ear was enclosed in a small paper packet (Table 1). This was to prevent pollination from other ears. Main ears of all 16 replicate plants were enclosed in all treatments. At harvest, which occurred before grains were hard, these ears were mapped for fertility, considering each floret and spikelet separately. A floret was fertile if it contained a grain, and infertile if the floret was gauged large enough to have a grain, yet was empty.

The control study is reported in this paper. The boron study, shown in Table 1 for comparison, appears in the companion paper. Glasshouse light was 31.6 ± 1.5 in the control study and 35.6 ± 1.9 mol/m²/d in the boron study between sowing and emergence of the second-last leaf ligule (FL – 1), and following that stage averaged 30.0 ± 1.4 and 42.1 ± 3.4 mol/m²/d respectively. Full light in the cabinets was 42.3 mol/m²/d in both studies.

Results

Environmental effects on growth and fertility of genotypes in different soil environments

Averaging across treatments in which full nutrient solution was applied daily, Fang 60 was taller than SW 41 (866 v. 833 mm, Table 2). It had around 15% more ears per plant (5.7 v. 4.9), though the ears were shorter (90 v. 106 mm long excluding the awns), with fewer spikelets (14.7 v. 16.6) and fewer florets (48.5 v. 57.3, Table 2). These florets, however, had marginally higher fertility (92% v. 88%). The combined effect on grain number was that Fang was some 12% less productive per main ear than SW 41 (45.0 v. 50.7).

Table 2 also shows that the effects of reducing boron rates had little effect on height, ears per plant and florets per ear, but ears were progressively shorter, were progressively more sterile and had progressively fewer grains per ear.

Light, temperature and humidity effects

There were no significant differences between genotypes in their responses to a reduction in light from 950 to 500 μmol/m²/s between emergence of the second-last leaf ligule and early grain filling. Plant height was marginally increased under less light (Table 3), ear number was reduced, and ears were shorter. However, the ears had the same spikelet number (this was expected as treatments were started after terminal spikelet initiation) but fewer florets, which were less fertile. The overall effect was an almost 40% reduction in grain number from a 47% reduction in light during this relatively short phase.

The overall effects of increasing mean temperature from 12° to 20°C were also large (Table 3). Plants were shorter, produced fewer ears and shorter main ears, and had fewer florets, which were less fertile. This led to a reduction in grain number of 16% per main ear. These changes were associated with a 43% reduction in the duration of the period between the start of the temperature

Table 1. Days after sowing of events in SW 41 and Fang 60 wheats

	Control	Boron
Sown	14 Feb. 95	31 Oct. 94
Days after sowing for:		
Seedling emergence	6	6
Fang 100% FL – 1	31	29
SW-41 100% FL – 1	32	31
Ears bagged*:		
Fang high temperature	43	43
SW-41 high temperature	45	†
Fang low temperature	52	50
SW-41 low temperature	57	†

* Ears were bagged at heading over several days but the day given is the average day when ears were approximately 90% emerged.

† Missing data.

treatment and ear emergence (from 23 to 13 days).

By contrast with temperature, the averaged effects of reducing humidity from 80% to 40% were very small and generally insignificant. However, because of significant interactions, using averages was not meaningful. Thus, although low light always reduced ear number, high temperature reduced ear number only at low humidity, not at high humidity. This is perhaps in keeping with ephemeral effects of aerial or soil water stress. Similarly, though shading always reduced floret numbers, RH had mixed effects. At high temperature, low RH apparently reduced floret number from 51 to 44 (though only under high light). Again, this could stem from brief water stress. By contrast, at low temperature, and under low light, low RH increased floret number from 47 to 51.

Interestingly, there were strong indications that high humidity, regardless of temperature, reduced floret fertility and grain number when light was only 21.6 mol/m^2/d, or equivalent to field conditions in early spring (Table 4). In keeping with earlier findings (Dawson and Wardlaw 1989), the reductions in fertility were greater at higher temperature.

Discussion

At the workshop on sterility held in Chiang Mai, Thailand, in 1994, a summary table was compiled of the suspected effects of environmental factors on sterility in the subtropics (Table 5). All participants, apart from the delegate from Pakistan, perceived low boron as a primary cause of sterility (Pakistan has few problems of the type of sterility discussed at the workshop). High temperature was seen as an important companion cause of sterility at Chiang Mai, and of some importance in Yunnan Province in China. It was not considered significant elsewhere. In Nepal, low temperature was identified as a contributor, whereas in Bangladesh, high humidity and low radiation were considered causes. Data in this paper lend support to the suggestions of high temperature, high humidity and low radiation. Even in the absence of limitations of boron in the growth medium, higher temperature increased sterility. The increases were marginal (3%–4%) under high radiation, but became important under low radiation (10%–15%), particularly at high humidity (Table 4). Low radiation was always of consequence to fertility in this experiment, reaching its greatest effect of 20% if temperature and humidity were both high. It also marginally reduced fertility at low temperature, again if humidity was high.

Though boron was added daily to the growth medium in the current control study, that does not rule out a limitation of boron at the sexual sites as being linked with sterility. In this study, increased mean temperature from 12° to 20°C increased the rate of development, reducing the period from emergence of the second-last leaf ligule to ear emergence from 23.0 to 12.5 days (Table 1). The number of days over which the sensitive stage of pollen meiosis occurred was possibly reduced by a similar proportion. This would halve the time plants could take up boron from the growth medium to fulfil the boron requirements of this phase. Increased humidity reduces transpiration

Table 2. Genotype comparisons. This represents the average response of all environment treatments for the study with boron non-limiting (control). There were no significant genotype by environment interactions. Also shown is the average genotype response for all environment treatments in the study with marginal boron (B1) and extremely low boron concentrations (B0)

Character	Fang 60 control	SW-41 control	Fang 60/ SW-41 % change	Mean of control plants	Marginal boron (B1)	'Zero' boron (B0)	B0/ control % change
Height (mm)	866	833	+4	850	855	857	0
Ears per plant	5.7	4.9	+16	5.3	5	5.6	+6
Ear length (mm)	90	106	–15	98	82	78	–20
Spikelets per main ear	14.7	16.6	–11	15.7	14	14	–11
Florets per main ear	48.5	57.3	–15	52.9	50	51	–4
Fertility main ear (%)	92	88	+5	90	34	1.6	–98
Grain number per main ear	45.0	50.7	–11	47.9	18.1	0.7	–99

Table 3. Effects of differences in light after emergence of the second-last leaf ligule, and effects of temperature and humidity (average response of Fang 60 and SW 41)

Light (μmol/m^2/s):	950	500	500/950 (% change)	Temperature 20°/12°C (% change)	Humidity 40%/80% (% change)
Character					
Height (mm)	845	864	+2	–16	–3
Ears per plant	6.2	4.6	–35	–10	–5
Ear length (mm)	103	96	–7	–8	0
Spikelets per main ear	15.7	15.7	0	0	0
Florets per main ear	59.9	46.8	–28	–9	0
Fertility main ear (%)	92.9	85.3	–9	–9	+4 *
Grain number per main ear	55.5	40	–39	–16	+2 *

* Interactions occurred

and the uptake of water (and boron) from the growth medium. A reduction of vapour pressure deficit from 11.7 to 3.9 mb, as in the two humidity treatments at high temperature (see Materials and Methods), would reduce transpiration to a third, from approximately 8.9 to 2.8 ng H_2O/cm^2/s (Rawson et al. 1977). Similarly, a reduction in radiation from 950 to 500 μmol/m^2/s would reduce stomatal conductance (and transpiration) by around 30% (Rawson ('Parameters'), these Proceedings). So the combined effects of low radiation and high humidity at high temperature (compared with high radiation and low humidity) could be to reduce daily boron uptake to 25%, and the duration of the period of development compared with that at low temperature to half. This means that plant transpiration integrated over the period of pollen meiosis would be reduced to 12% by these treatments. The most severe condition for sterility in the absence of boron limitation in the growth medium was high humidity combined with high temperature and low radiation. Clearly, in a low boron soil, this combination of environmental factors could become highly significant to fertility.

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Table 4. Effects of humidity differences after emergence of the second-last leaf ligule on floret fertility at lower light (22.3 mol/m^2/d) (average responses of Fang 60 and SW 41)

	27°/13°C			17°/7°C		
	40% RH	80% RH	(% change)	40% RH	80% RH	(% change)
Character						
Height (mm)	791	765	+3	953	949	0
Ear length (mm)	92	89	+3	101	99	0
Florets per main ear	44	45	0	51	47	+8
Fertility main ear (%)	84	74	+13	93	89	+5
Grain number per main ear	37	33	+12	48	42	+14

Table 5. Summary of perceived effects of several factors on sterility in wheat. Numbers indicate rankings of importance (from the workshop on sterility in wheat held at Chiang Mai University, 1994)

	Thailand	Nepal	Bangladesh	Pakistan	Yunnan
Soil pH	✓	✓ 2	✓		
Soil boron	✓ 1	✓ 1	✓ 2		✓ 1
Soil N	☆	✓ 4	✓		
Low light			✓ 2	☆	
Water excess	✓	✓ 3	✓ 3	✓	✓ 2
Water deficit	✓ 2		✓ 4	✓	
Low temperature		✓ 1	✓ 4	☆	
High temperature	✓ 1			✓	✓ 3
High humidity			✓ 1	✓	✓ 4
Salinity				✓	

✓ = perceived effect
☆ = suspected effect

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Effects of Boron Limitation in Combination with Changes in Temperature, Light and Humidity on Floret Fertility in Wheat

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Abstract

The aim of this study was to determine whether the effects of low boron in causing floret sterility are accentuated by environmental variables. Plants of two genotypes of wheat (Fang 60 and SW 41) were grown in a glasshouse (27°/13°C) in sand culture using a boron-free nutrient solution until the ligule of the second-last leaf on the main shoot had emerged. They were then transferred to artificially lit growth cabinets and exposed to all combinations of 27°/13°C or 17°/7°C temperature, 80% or 40% relative humidity, marginal or zero boron solution, and 950 or 500 µmol/m²/s light until approximately one week after anthesis. Some plants remained in the glasshouse throughout and others were transferred to the cabinets only until ear emergence (short transfer treatment). The resultant degree of floret sterility was determined during mid grain filling.

Zero boron caused almost complete sterility regardless of genotype or the environmental treatment applied. Marginal boron reduced fertility to around 37% whereas a full boron solution resulted in 90% fertility. Lower light alone reduced fertility by around 8%, but when in combination with a marginal boron supply it amplified the boron effect by some 60%. So these two sterility factors were much more powerful in combination than separately, and the effects were not simply additive. Reduced light had the most deleterious effect at high temperature. There was no evidence that high humidity amplified the effects of marginal boron. Indeed, the reverse applied. This unexpected response is discussed.

Plants remaining in the glasshouse throughout performed the same as plants in the most similar artificially lit treatment, indicating that light quality in the growth chambers did not affect fertility. The short transfer treatment produced equivalent results to the full-duration transfers, demonstrating that the effects of boron and environment on sterility occurred before anthesis.

THE companion paper to this one (Rawson et al., these Proceedings) described the effects of temperature, light and humidity on the performance of wheat plants (genotypes Fang 60 and SW 41) when boron was non-limiting. It was shown that production of grain could be considerably altered by those environmental parameters, even though they were changed only during the period from first appearance of the flag leaf to early grain set. The most deleterious combination of weather parameters was high temperature, low radiation and high humidity. The effects were on number of ears, number of florets per ear (low radiation particularly) and floret fertility, which fell to around 70%. From that controlled environment work it was concluded that weather can alter fertility even when boron in the soil is plentiful.

The present paper examines whether the deleterious weather parameters still induce sterility when boron is limiting, and whether they act to amplify the boron effect. As discussed in the companion paper, boron is moved primarily with the transpiration stream (Kohl and Oertli 1961), so it might be argued that any environmental factors that reduce transpiration would also reduce the flow of boron into and through the plant. In a low boron soil this could be enough to result in increased ear sterility, as boron is required for fertility of the generative organs. Environmental factors expected to increase the negative effects of low soil boron would include high temperature, which accelerates the rate of plant development, thus leaving less time for boron to be imported for each developmental phase; high humidity, which reduces potential transpiration and possibly boron movement; and low radiation, which reduces stomatal aperture and associated transpiration rate. This paper tests these assumptions by comparing ear sterility of plants grown at low and high temperature, low and high humidity, and low and high radiation, all with or without severely limiting soil boron. To make the work comple-

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mentary to that in the companion paper where boron was non-limiting, the two boron rates used here were severely limiting and marginal (see Table 2 in the companion paper). Exactly the same environmental treatments were used as in the companion paper. The timing of treatment imposition was the same; that is, when the ligule of the second-last leaf had emerged (leaf 6 or 7). At this time, plants were moved from a common glasshouse condition, in which no boron had been provided in the nutrient solution, into artificially lit growth cabinets, where the different environments were applied and the application of a marginal amount of boron began.

As in the companion paper and in the other experiments done by the ACIAR group, wheat genotypes Fang 60 and SW 41 were used. These are respectively tolerant of and sensitive to low concentrations of soil boron (Rerkasem and Loneragan 1994). The companion paper found the two genotypes to respond very similarly to weather parameters when boron was not limiting.

Materials and Methods

Plants of two genotypes of wheat, Fang 60 and SW 41, both from Thailand, were grown in a glasshouse in the CERES phytotron, Canberra, Australia (Morse and Evans 1962). The glasshouse temperature was maintained between extremes of 27° and 13°C following a daily sine curve. Maximum temperature occurred at 1 p.m. The growth medium was a sand, which had been prewashed for several days, contained in 100 × 150 mm pots (volume 1.18 L) to which was added a nutrient solution (Table 1) each morning and afternoon. All pots were washed in dilute acid followed by boron-free water before planting. There were 16 pots of each genotype in each treatment split into four blocks (four plants per block). While plants remained in the glasshouse and before the environment treatments began, they were watered with a boron-free solution. Plants provided with a full nutrient solution throughout growth were part of the companion study (Rawson et al., these Proceedings).

The treatments of the two genotypes were two boron rates (zero and marginal) by two temperatures by two humidities by two light regimes. One set of plants remained in the initial glasshouse condition throughout. Treatments began when the ligule emerged on the leaf before the flag leaf. This leaf number was determined by dissection of some plants, which were then discarded. At that stage, plants were moved from the glasshouse to artificially lit growth cabinets maintained at 27°/13°C (as in the glasshouse) or 17°/7°C sine curve. Both high and low temperature regimes were set for 80% and 40% relative humidity (four cabinets). In the high temperature treatment, actual mean daily RHs were 83 ± 0.1% and 49 ± 0.1% (vapour pressure deficits of 3.8 and 11.7 mb respectively), and in the low temperature treatment they were 84 ± 0.1% and 67 ± 1.3% (VPDs of 2.1 and 4.5 mb). The two light regimes were 950 and 500 μmol/m^2/s maintained for 12 hours each day. The lower light regime was achieved by the use of frames covered with aluminium-stranded cloth placed over half the plants in each cabinet.

As each main ear emerged at least 50% above the flag leaf, and well before anthesis occurred, the ear was enclosed in a small paper packet. This was to prevent pollination from other ears. Main ears of all 16 replicate plants and many of the subsidiary ears were enclosed in all treatments. At harvest, which occurred before grains were hard, these ears were mapped for fertility, considering each floret and spikelet separately. A floret was fertile if it contained a grain, and infertile if the floret was gauged large enough to have a grain, yet was empty (Bagga and Rawson 1977).

Results

Effects of boron on fertility

If there was no boron in the nutrient solution (B0) during the period of flag leaf expansion to anthesis, as in this study, ears were made almost completely sterile (Table 2), regardless of other environmental parameters. If boron was supplied at a marginal level (B+) during this period, fertility rose to around 37%, even though no boron had been provided during the vegetative phase. But if boron was sufficient throughout (B++), fertility was at least 70% in the most limiting environment and 98% in the best. Consequently, boron had a dominant effect on fertility in these studies. Because boron had such an overwhelming effect in the B0 treatment, that treatment does not help to assess interactions between boron and the environment. However, the B+ treatment is useful.

The lesson from the GH and ST treatments (Table 2) is that plants in the glasshouse performed

Table 1. Composition of the nutrient solution. Stock solutions 1 to 4 and all water used in low boron tanks were purified through a column of borate-specific resin (Amberlite, IRA-743, Sigma Chemical Co.). Nutrient solution pH was 6.88

Stock	Chemical	Mass in the stock solution	Stock solution (L)	Element	Final conc. (ppm)
1	$Ca(NO_3)_2 \cdot 4H_2O$	9.6 kg	20	N	114
2	$(NH_4)_2HPO_4$	1.371 kg	20	P	16
3	KNO_3	6.118 kg	40	K	118
4	$MgSO_4 \cdot 7H_2O$	2.536 kg	20	Mg	13
5	$FeSO_4 \cdot 7H_2O$	50 g	5	Fe	2
	EDTA	66 g			
	NaOH	13 g			
6	$MnCl_2 \cdot 4H_2O$	3.99 g	5	Mn	0.056
	$ZnSO_4 \cdot 7H_2O$	2.20 g		Zn	0.025
	$CuSO_4 \cdot 5H_2O$	0.51 g		Cu	0.007
	$Na_2MoO_4 \cdot 7H_2O$	0.30 g		Mo	0.006

very similarly to their transferred equivalents (27°/13°C, no shade and 80% RH). These plants with zero boron were fully sterilised and those on a marginal dose approximated 50% fertility. This comparison indicates that light quality in the chambers was acceptable and that the chambers themselves did not have any spurious effects on sterility.

The short transfer from the glasshouse to the 27°/13°C treatment with low humidity and without shade also paralleled the response of plants in the full treatment. From this we can also draw some confidence in the overall data set. We can also conclude that the treatment effects that increased sterility had already occurred by ear emergence. Plants in the main study remained in their regimes until at least seven days after anthesis, or around two weeks more. Thus, the humidity effects were not effects during anthesis.

Effects of reduced light × boron on fertility

Table 3 shows how fertility of the main ears was reduced by shading by an average of only 8.3% in the treatment with adequate boron (100 – 91.7 = 8.3), whereas in the marginal boron treatment (B+), shading reduced fertility by more than 60%. Most surprisingly, the genotype Fang 60, which is little affected by low boron in the field (Rerkasem and Loneragan 1994), was more affected by shading than SW 41 when boron was limiting. The effects of shading were more deleterious at higher temperature (66%) than at lower temperature (48%). There was limited evidence also that shading reduced fertility more at higher humidity, though only at lower temperature.

Effects of increased temperature × boron on fertility

Table 4 shows that increased temperature had little overall effect on percentage fertility when boron was adequate, but reduced fertility considerably when boron was marginal, particularly under low radiation.

Effects of increased relative humidity × boron on fertility

There was no evidence that high humidity accentuated the effects of limiting boron on sterility, as was expected from theory. In fact, the reverse situation generally applied: there was less sterility under boron limitation. This contrasts with the effect of high humidity reducing fertility at high temperature under low radiation when boron was adequate.

Discussion

The expectation from this work was that the negative effects of low boron on fertility would be amplified by growing plants at high temperature during pollen meiosis (between first appearance of the flag leaf and ear emergence), by maintaining

Table 2. Percentage fertility in main ears of Fang 60 and SW 41 plants provided with no boron (B0), a marginal amount (B+), or an adequate amount (B++) and grown under two temperatures, two humidities and two light levels after emergence of the second-last leaf ligule

			B0			B+			B++		
Temp.	RH	Light	Fang 60	SW 41	Mean	Fang 60	SW 41	Mean	Fang 60	SW 41	Mean
27°/13°C	80	high	0.0	0.1	0.1	48.4	50.9	49.7	90.7	90.7	90.7
		low	1.9	2.7	2.3	5.7	19.3	12.5	74.6	74.3	74.5
	40	high	0.2	0.3	0.3	36.3	38.9	37.6	96.7	92.5	94.6
		low	0.6	0.0	0.3	1.2	15.8	8.5	96.0	91.0	93.5
17°/7°C	80	high	4.7	0.5	2.6	52.3	53.9	53.1	97.9	91.3	94.6
		low	5.0	0.3	2.7	17.5	30.5	24.0	93.7	85.1	89.4
	40	high	0.0	0.0	0.0	56.9	55.7	56.3	93.0	90.1	91.6
		low	5.0	0.0	2.5	29.0	37.7	33.4	87.7	79.8	83.8
27°/13°C	GH	high	0.1	0.1	0.1	49.2	52.4	50.8	98.5	97.0	97.8
	ST	high		0.0	0.0		40.5	40.5			
Mean					1.3			36.6			90.0

GH = plants that remained in the glasshouse with natural light throughout growth (i.e. no shading).
ST = plants that were transferred to the artificially lit cabinet at the prearranged stage but were transferred back to the glasshouse at heading time ('short transfer').

lower radiation, and by holding a high relative humidity. The perceived effects of these treatments would be, first, to accelerate development, leaving less time for the plant to take up boron and move it to the generative areas; and second, to reduce the uptake of boron by reducing both transpiration rate (low radiation) and evaporation (high humidity).

The expectations were partially borne out. High temperature accelerated development (see companion paper) and certainly reduced fertility when boron was marginal (Table 4). There was only a minimal effect when boron was plentiful. Low radiation dramatically accentuated the low boron effect as predicted (Table 3), particularly at high temperature.

High humidity effects did not follow expectations, however. In fact, high humidity reduced the effect of low boron on fertility. All we can suggest to explain this response is that high humidity reduced the diurnal water stress that plants might have been suffering, and this in turn reduced stomatal closure, which increased boron uptake. Plants were grown in sand and provided with water twice each day, but the pots were small. Unfortunately, we cannot confirm this suggestion as we did not measure stomatal conductance. The point remains, though, that the response to humidity will always depend on whether the plants are stressed or not. The same argument will apply to responses to light and temperature. High light, high temperature and water stress are often linked in the field, and it is very difficult to separate their effects on boron uptake unless extensive measurements are taken to characterise both the environment and the plant's degree of stress.

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Table 3. Effect of shading in the B+ and B++ treatments on fertility. Data are presented as (fertility % at 500 μmol/m^2/s) ÷ (fertility % at 950 μmol/m^2/s) × 100

		B+			B++		
Temp.	RH%	Fang 60	SW 41	Mean	Fang 60	SW 41	Mean
27°/13°C	80	11.8	37.9	25.2	82.2	81.9	82.1
	40	3.3	40.6	22.6	99.3	98.4	98.8
17°/7°C	80	33.5	56.6	45.2	95.7	93.2	94.5
	40	51.0	67.7	59.2	94.3	88.6	91.5
Mean		24.9	50.7	38.1	92.9	90.5	91.7

Table 4. Effect of increasing temperature in the B+ and B++ treatments on fertility. Data are presented as (fertility at 27°/13°C) ÷ (fertility at 17°/7°C) × 100

		B+			B++		
RH%	Light	Fang 60	SW 41	Mean	Fang 60	SW 41	Mean
80	high	92.5	94.4	93.5	92.6	99.3	95.9
	low	32.6	63.3	52.1	79.6	87.3	83.3
40	high	63.8	69.8	66.8	104	102	103
	low	4.1	41.9	25.5	109	114	111
Mean		48.3	67.4	59.5	96.4	101	98.5

Table 5. Effect of increasing relative humidity in the B+ and B++ treatments on fertility. Data are presented as (fertility at 80%) ÷ (fertility at 40%) × 100

		B+			B++		
Temp.	Light	Fang 60	SW 41	Mean	Fang 60	SW 41	Mean
27°/13°C	high	133	130	132	93.8	98.1	95.9
	low	475	122	147	77.7	81.6	79.6
17°/7°C	high	91.9	96.8	94.3	105	101	103
	low	60.3	80.9	72.0	106	106	106
Mean		190	107	111	95.9	96.9	96.4

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Effects of Boron Deficiency and Low Temperature on Wheat Sterility

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Abstract

Wheat exhibits sterility in many parts of subtropical and tropical Asia. Boron deficiency is believed to be the cause of sterility in many, but not all, cases. This creates the need for standards to allow B deficiency to be diagnosed and distinguished from other causes of sterility. This study was designed to investigate the responses of functional indicators of B requirements, namely leaf blade elongation rates and potassium leakage rates, to B supply (0 and 10 µM B) and night temperature (ambient: > 10°C and low: > 5°C). An objective of the study was to develop diagnostic and prognostic standardsfor B deficiency, based on the functional B requirements for leaf elongation and membrane permeability.

Although the interruption of B supply (–B) significantly decreased B concentrations in leaf blades and ears, it had no consistent effect on rates of leaf blade elongation or leaf K leakage in the two cultivars of wheat tested at either the vegetative or the reproductive stage. Low night temperature also had little effect. However, the grain set index (GSI) was significantly decreased by the –B treatment. Low night temperature had no effect on GSI in +B plants. In –B plants, ambient night temperature decreased GSI apparently by accelerating ear development, so that critical stages of grain set coincided more with the deficiency of B than in –B plants exposed to low night temperatures.

BORON (B) is an essential micronutrient for the growth of plants. Some grasses, such as wheat, have a much lower B requirement for normal growth than dicots (Dugger 1983). Nevertheless, B deficiency causing yield loss has been documented in wheat in southern and eastern Asian countries such as Bangladesh, China, Nepal, India and Thailand (Rerkasem et al. 1993).

Boron deficiency affects the growth and function of male or female reproductive organs of wheat, leading to the failure of fertilisation and grain setting (Rerkasem et al. 1993) and eventual yield loss. B deficiency causes the poor development of anthers and pollen and germination failure of pollen, owing to insufficient B supply in the pollen or in the stigma and style (Cheng and Rerkasem 1993).

Although there is an increasing understanding of the role of B deficiency in wheat sterility, the detection of B deficiency in wheat plants at the reproductive stage often allows no time for correction of the problem. Wheat vegetative growth is insensitive to B deficiency. There are usually no symptoms in the leaves and no significant growth reduction. Vegetative growth is therefore not a reliable diagnostic indicator of B deficiency. In addition, rate of dry matter accumulation responds to the declining B supply more slowly than leaf B concentrations (Kirk and Loneragan 1988). As a result, it is advisable to explore physiological responses of shoots to B deficiency for its early diagnosis.

Boron plays both structural and functional roles in plant cells (Loomis and Durst 1992; Parr and Loughman 1983). Boron is an essential component of cell wall structure (Loomis and Durst 1992) and B deficiency inhibits cell division and elongation (Hu and Brown 1994). Boron deficiency disturbs membrane integrity and increases membrane permeability (Cakmak et al. 1995; Parr and Loughman 1983).

Based on these functional roles of B in plant cells, it is presumed that leaf elongation and leaf K leakage are sensitive parameters by which to diagnose B deficiency in wheat plants. The response of leaf blade elongation rates to B deficiency has been successfully used to set a critical B concentration for the diagnosis of B deficiency in black gram (Noppakoonwong et al. 1993). In sunflower, leaf K leakage rates were closely correlated with leaf B concentrations

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(Cakmak et al. 1995).

Wheat production is increasing in the warmer areas of southern and eastern Asia, such as Bangladesh, Nepal, China and Thailand (Rerkasem et al. 1993). Field observation has shown that wheat plants grown in these areas might be exposed to low night temperature just before or during anthesis, enhancing the failure of grain set (Pant, pers. comm.).

Several reports appear in the literature linking low temperature damage in plants and B deficiency (Shorrocks 1991). These reports are limited to observations of increased damage to shoots by frost or low temperature when plant B status is low, and in some cases, alleviation of the injury with foliar B sprays. Experimental evidence that low temperatures increase sensitivity to B deficiency is limited to one brief report by Parr and Loughman (1983). Parr and Loughman examined the response of P uptake by *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. However, below 20°C there was a distinct inflection in the curve, which implied a temperature-dependent change in membrane conformation from a fluid to a gel. For plants grown in tropical and subtropical regions, low temperature even above freezing point might cause a change in membrane properties and enhance membrane permeability (Simon 1974). What had not been previously reported was the finding of Parr and 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-sufficient solutions. These limited results imply that plants with low or deficient B supply might be more sensitive to cold temperature damage to membranes of growing tissues than plants with sufficient B.

In 1994, at Tonglu in Zhejiang Province, China, we observed oilseed rape plants showing symptoms of frost damage to the leaves. This was in late March, some 10 to 14 days after snowfalls that remained on the ground for two days. It was only in plots without B fertiliser that frost damage occurred; plants treated with B fertiliser at sowing were free of the symptoms. Thus it appears that leaf tissue of oilseed rape was more sensitive to frost damage when low in B. The converse conclusion, that low temperature increases internal B requirements, has not been demonstrated.

Interesting as these observations are, their relationship to B deficiency and to internal B requirements is not clear. Episodes of low temperature could be the cause of site-to-site and year-to-year variation in internal B requirements of wheat, and therefore in grain set. Further studies to establish a meaningful causal link between low temperature damage and plant B status would be particularly useful. Controlled environment studies would appear to be necessary to establish such a link. Field demonstration of the significance of a low temperature effect is also necessary.

The objectives of the present study were to examine effects of B deficiency and low night temperature on leaf blade elongation and leaf K leakage, and to establish a relationship between these responses and leaf B concentrations. On the basis of this relationship, the study aimed at estimating diagnostic standards for B deficiency in wheat vegetative growth, and prognostic standards for predicting the sterility of florets and grain set failure in wheat plants during the reproductive stage. It was hypothesised that low night temperature might exacerbate B deficiency in wheat plants subjected to low B supply. This paper reports the responses of leaf blade elongation rates, leaf K leakage, B concentrations, spikelet fertility and grain set index to B deficiency and low night temperature for wheat plants at vegetative and reproductive stages.

Materials and Methods

Plant culture

Wheat plants were grown in solution culture in a glasshouse. The full-strength basal nutrient solution used initially contained the following chemicals. Concentrations in parentheses are µmol/L: NH_4NO_3 (2000), KNO_3 (2800), $Ca(NO_3)_2 \cdot 4H_2O$ (1600), $MgSO_4 \cdot 7H_2O$ (1000), KH_2PO_4 (100), and K_2HPO_4 (100), FeEDTA (100), NaCl (8), $ZnSO_4 \cdot 7H_2O$ (2), $MnSO_4 \cdot H_2O$ (2), $CuSO_4 \cdot 5H_2O$ (0.5) and $Na_2MoO_4 \cdot 2H_2O$ (0.08). Water used for making up the solutions and the macronutrient stock solutions were purified with B-specific resin (IRA-743, Sigma Chemical Co.). Only analytical grade chemicals were used to make up the solutions. The initial pH in the solution was about 6. The pH was buffered at 7.0 to 7.5 by adding 0.1 g $CaCO_3$ to each pot of solution.

The programmed nutrient addition technique (Asher and Edwards 1983) was used to supplement all nutrients during plant growth, except for B during the B treatment period. The following nutrient concentrations were assumed to be adequate in whole shoots: 4.5% N, 0.4% P, 3.0% K, 0.3% Ca, 0.3% S, 0.2% Mg, 50 mg/kg Fe, 20 mg/kg Mn, 20 mg/kg Zn, 5 mg/kg B, 3 mg/kg Cu and 0.5 mg/kg Mo. The following model was used to predict plant dry matter at a given day:

$$Y = A \times \log_{10}(A) + e^{(RGR \times T)}$$

where Y is the predicted dry weight per plant, A is the existing dry weight (g per plant), RGR is relative growth rate (g/g/day), and T is the number of days. The amounts of nutrients and B needed were calculated by the 'Nutradd' software (Asher and Blamey 1987). The RGR was determined by sequentially harvesting plants in extra pots of the +B treatment.

Experiment 1—Reproductive stage

This experiment was designed to investigate the responses of the permeability of leaf cell membranes (measured as K leakage) and leaf blade elongation in plants at the reproductive stage to the experimental treatments, and to attempt to correlate the responses with pollen viability and grain set index.

Wheat seeds (*Triticum aestivum* cv. SW 41, from Thailand) were soaked in aerated $CaSO_4$ solution (2 mM) for four days in the dark at room temperature (10°–16°C). The germinated seedlings were then transplanted into a plastic tray containing 8 L of one-third strength basal nutrient solution (with 5 μM B) and placed in the glasshouse. After five days in the trays, the seedlings were transplanted into pots containing 5 L of full strength nutrient solution with 5 μM B. Nine seedlings, with about 1½ leaves each, were planted into each pot. The pots were randomly positioned in a temperature-controlled water bath set at 18 ± 1°C. The pots were repositioned every two days to minimise positional effects on growth.

At 13 days after transfer (DAT), plants were thinned to eight per pot. Dry weights of the thinned plants were recorded at transfer and at 13 DAT, and relative growth rates were calculated using the Nutradd software (Asher and Blamey 1987). Calculated amounts of nutrients were added to the solutions on 15, 22, 44 and 64 DAT. The healthy appearance of the plants in the B-sufficient pots indicated that the nutrients added were adequate for plant growth.

At 31 DAT (about 8th leaf stage), the B and night temperature treatments were begun using two sets of four replicates in each treatment. The B treatments were 0 μM (–B) and 10 μM (+B) H_3BO_3. The night temperature treatments were ambient glasshouse temperature (> 10°C) and low temperature (> 5°C). The detailed glasshouse environmental conditions are shown in Table 1. A recorded example of the low night temperature profile is shown in Figure 1. During the treatment, the low night temperature averaged 9.2°C (max. 13.7° – min. 5.7°). Low temperatures were imposed by transferring pots every evening to a temperature-controlled room. The room was programmed so that temperatures decreased progressively from ambient at 5:30 p.m. to a minimum of 6°C at 6 a.m. Plants were transferred out of the cold room each day at 7 a.m. to the glasshouse. During the day both sets of plants experienced the same environmental conditions. The plants were exposed to the B and night temperature treatments for 18 days and then B was resupplied to the –B plants until grain set.

The length of the ninth leaf of a main stem was measured daily over seven consecutive days in three plants per replicate from its emergence to its maximum length for the determination of elongation rate. From one set of the plants, the youngest emerging blades (YEB) and the blades immediately older than YEB (YEB + 1) were sampled from the main stems of two plants per replicate for the determination of B concentrations at 1, 3, 7, 12 and 18 days after the start of treatment. At 12 and 18 days after the start of treatment, ears of the main stems were also harvested for the determination of B concentrations. Plant growth stage at each harvest is given in Table 2.

For the determination of leaf K leakage in YEB of the main stem, two plants per replicate were sampled from the other set of plants. The leaves were cut off at the base of the emerged blades. As B deficiency affects growing tissues more than mature ones, the basal part of the YEB was considered to be the most sensitive to B deficiency. The leaf segment up to 5 cm from the base was cut into 1 cm strips. After being washed in three changes of triple-deionised (TDI) water, these leaf strips were placed in a plastic container with 10 mL TDI water and gently shaken for two hours (10 a.m. to 12 noon) at glasshouse temperature in

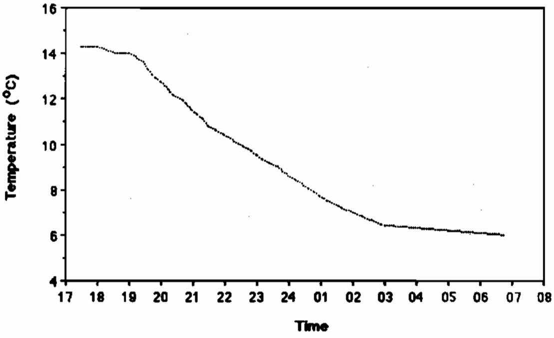

Figure 1. A example of a night temperature (°C) profile in the cold room used to expose wheat plants to low temperature. The temperature was set to decrease gradually between 5:30 p.m. and 6 a.m. the next day from ambient temperature down to 6°C.

the light (Navari-Izzo et al. 1989). The solutions were sampled for the determination of K leaked out of the leaf strips. The leaf strips were frozen at –20°C and thawed at room temperature for total membrane disruption in the leaf cells. The thawed leaf samples were incubated in 20 mL TDI water overnight and K concentrations in the incubation solutions were determined by inductively coupled plasma (ICP) spectrometry.

Ears of the main stems were harvested for the determination of grain set index 52 days after the start of treatment, when full grains were observed in ears of the +B plants.

Experiment 2—Vegetative stage

Wheat cultivar Wilgoyne was used to investigate effects of B supply and low night temperature on responses of leaf blade elongation, leaf K leakage and leaf B concentrations at the vegetative stage for the diagnosis of B deficiency. Wheat seedlings were prepared as described for Experiment 1. Wheat seeds were soaked in the dark at room temperature (about 18°–25°C) in aerated $CaSO_4$ solution for three days until germination. Uniformly germinated seedlings were transplanted into a plastic tray with 8 L of one-third strength nutrient solution. After being acclimatised in the glasshouse for six days, ten randomly selected plants were transferred into each plastic pot, which contained 5 L of complete, full-strength nutrient solution.

The treatments of B supply and low night temperature were applied to the plants at 26 DAT. Boron treatments were 0 (–B) and 10 (+B) µM and the temperature treatments were ambient glasshouse temperature (16°–20°C) and low temperature (5°–15°C). In the –B treatment, B-specific resin (6 g air-dry per pot) was placed in

Table 1. Environmental conditions in the glasshouse during the treatment periods of experiment 1 and 2

		Air T (°C)	Water T (°C)	RH %	Daily average light intensity (µmol/m^2/s)	Total radiation (MJ/m^2/day)
Experiment 1 (SW 41)						
Day	Mean	21.5	18.3	69	268	6.61
	Maximum	25.2	21.1	83	760	9.41
	Minimum	15.5	16.2	59	64	1.54
Night	Mean	17.3	16.9	80		
	Maximum	21.3	17.9	84		
	Minimum	15.8	16.9	75		
Experiment 2 (Wilgoyne)						
Day	Mean	21.9	19.6	73	291	7.14
	Maximum	25.2	23.0	85	758	8.65
	Minimum	16.0	16.5	64	198	5.28
Night	Mean	17.9	17.5	81		
	Maximum	21.5	18.7	84		
	Minimum	15.8	16.9	75		

the solution to minimise B concentrations in solution. Each treatment was replicated four times. The detailed glasshouse environmental conditions are shown in Table 1. A recorded example of night temperature profile in the cold room is shown in Figure 1. During the treatment, the low night temperature averaged 10°C (max. 14.2° – min. 7.1°) in the cold room.

Potassium (K) leakage was measured in the youngest emerging blades. Two plants per pot were sampled for YEB from the main stems of one set of plants at 0, 3, 6, 9 and 12 days after the start of treatment. The measurements were conducted in the same way as in experiment 1.

The length of the seventh leaf of a main stem was measured daily over seven consecutive days in three plants per replicate from their initial emergence to their maximum length for the determination of their elongation rate.

In the other set of plants, the YEB and YEB + 1 blades were sampled from the main stems of two plants per replicate for the determination of B concentrations at 0, 3, 6, 9 and 12 days after the start of treatment. Plant growth stage at each harvest date is given in Table 2.

Boron determination

The samples were dried at 70°C to constant weight and digested with concentrated nitric acid at 140°C. Boron concentrations in the digest solutions were determined by ICP spectrometry (Zarcinas et al. 1987).

Data analysis

Two-way analysis of variance was applied to the data to detect the effects of B supply and night temperature treatments on leaf blade elongation rates, leaf K leakage and B concentrations.

Results

Leaf blade elongation and K leakage— Experiment 1

At the start of treatments, B concentrations in leaf 8 were relatively low, at 3 to 5 mg/kg (Tables 3a, 3b). Subsequently, in +B solutions, leaf B concentrations in plants at ambient night temperatures increased to 9 mg/kg at 12 days after the start of treatment (DAS) and then declined markedly at 18 DAS to 3 mg/kg. In +B plants at low night temperature, B concentrations in leaf 8

Table 2. Plant growth stages at each harvest in experiments 1 and 2

Harvest	Date	Day	Plant stage
Experiment 1 (SW 41—reproductive stage)			
	9 June	0	8th leaf emerging
Harvest 1	10 June	1	8th leaf emerging, 7th leaf fully emerged
Harvest 2	12 June	3	8th leaf fully emerged, 9th (flag) leaf emerging
Harvest 3	16 June	7	Flag leaf half emerged
Harvest 4	21 June	12	Flag leaf ligule emerged, ear size ≈ 4 cm
Harvest 5	27 June	18	Late booting in Ta plants
(B resupply)			Mid booting in Tl plants
	6 July	27	Anthesis in Ta plants
	12 July	33	Anthesis in Tl plants
Harvest 6	31 July	52	Late milky to soft dough. Main stem grain full
Experiment 2 (Wilgoyne—vegetative stage)			
Harvest 1	23 June	0	6th leaf $^1/_3$–$^1/_2$ emerged
Harvest 2	26 June	3	6th leaf fully emerged, 7th leaf $^1/_4$–$^1/_3$ emerged
Harvest 3	29 June	6	7th leaf $^4/_5$ emerged
Harvest 4	2 July	9	7th leaf fully emerged, 8th leaf emerging
Harvest 5	5 July	12	8th leaf $^1/_2$ emerged

Ta = ambient night temperature, Tl = low night temperature ranged from 4 to 8 mg/kg over the period 3–12 DAS and, as in plants at ambient night temperature, dropped at 18 DAS to 3 mg/kg.

In –B treatments, B concentrations in leaf 8 declined strongly between 1 and 3 DAS and, by 7 DAS, had declined to 2 to 3 mg/kg, where they remained.

In leaf 9, which emerged at 7 DAS, B concentrations in –B plants were 1 to 1.5 mg/kg at emergence and remained there. By contrast, B concentrations in leaf 9 of +B plants were 3 to 7 mg/kg.

At 12 and 18 DAS, low temperature increased B concentrations in the ears of +B plants, and decreased them in –B plants.

No obvious symptoms of B deficiency or injury caused by low temperature were observed in the –B plants or low-temperature-treated plants.

Although the removal of B supply decreased B concentrations to as low as 1 mg/kg dry matter, it did not induce any significant increase in K leakage out of the newly emerged leaf blades (Table 4). The effects of low temperature on leaf K leakage were not consistent over time.

The effects of –B and low temperature on leaf blade elongation rates of the ninth leaf were generally not significant (Table 5).

Leaf blade elongation and K leakage—Experiment 2

Boron concentrations in the YEB were decreased only by the –B treatment, not by low temperature. There was no interaction between –B and low temperature on B concentrations in the leaves (Table 6).

The treatments of –B and low night temperature generally caused no response in K leakage from YEB, except that –B significantly increased K leakage from YEB at ambient temperature compared with low temperature at 6 DAS (Table 7). The elongation rates of YEB were not consistently affected by the B or temperature treatments (Table 8). A significant decrease in leaf blade elongation rates caused by low temperature was observed at 2–3 DAS, but the reverse applied at 4–6 DAS. The young leaves became flaccid when returned to the glasshouse after being exposed to low night temperature.

Spikelet fertility and grain set index

The interruption of B supply significantly decreased spikelet fertility and grain set index (GSI) in SW 41 plants (Table 9, Fig. 2). There was slower ear development in the low night temperature treatment than at ambient night temperature. The low temperature treatment had no effect on spikelet fertility or GSI of plants with B, but increased them in plants without B. In comparison, the numbers of grain and florets in each spikelet of both –B and +B plants was increased by the low temperature treatment (Fig. 2). These effects of B and night temperature treatments occurred mostly in the central florets (spikelets 3–17).

Discussion

The present study aimed at exploring sensitive physiological responses of wheat to B deficiency and their relationship to B concentrations in shoot parts. However, the relationship between rates of leaf blade elongation and leaf K leakage and concentrations of B in leaf blades and ears could not be established, owing to the lack of response of these two variables to B withdrawal (–B) and low night temperature.

The results indicate that the growth of vegetative parts requires very low internal B supply at both the vegetative and reproductive stages. A previous study with SW 41 (Rerkasem et al. 1993) showed that withdrawing B supply for 12 days also had little effect on the length of YEB. For wheat plants during the vegetative stage, a B concentration of 3 mg/kg dry matter or greater was adequate for growth (Reuter and Robinson 1986). In the present study, –B treatment decreased B concentrations in the YEB to around 1 mg/kg dry matter in the plants at vegetative (Wilgoyne) and reproductive (SW 41) stages, but did not have any effect on rates of leaf blade elongation and leaf K leakage from the YEB. In contrast, dicot crops have much higher B requirement for their growth and much higher critical B concentrations than the adequate B concentrations for wheat (Reuter and Robinson 1986). For example, critical B concentrations in the youngest open leaves (similar to the YEB in wheat plants) of canola plants are as high as 10 to 14 mg/kg dry matter (Huang and Bell 1994). The low internal B requirement of wheat plants gives rise to the practical difficulty of establishing the changes in leaf blade elongation and leaf K leakage rates of YEB in response to the narrow range of leaf B concentrations from deficiency to adequacy.

Table 3a. Boron concentrations (mg/kg dry matter) in the eighth and ninth leaves of SW 41 wheat for selected days after starting the treatment (DAST). Plants were subjected to a factorial combination of temperature and B supply treatments at the reproductive stage. The values are means of four replicates, followed by standard deviation in parentheses

Treatment		1 DAST	3 DAST	7 DAST	12 DAST	18 DAST
Eighth leaf	–B, Tl	3.45 (0.84)	2.82 (0.78)	1.88 (0.50)	2.44 (0.24)	1.92 (0.34)
	–B, Ta	3.76 (1.31)	2.39 (0.26)	2.18 (0.25)	3.13 (0.86)	1.88 (0.56)
	+B, Tl	5.10 (0.42)	4.55 (0.25)	4.05 (0.70)	7.64 (1.04)	3.42 (0.18)
	+B, Ta	3.67 (0.28)	6.38 (0.68)	7.09 (0.47)	9.27 (0.95)	3.30 (0.82)
Ninth leaf	–B, Tl		ND	0.93 (0.65)	1.38 (0.74)	1.08 (0.20)
	–B, Ta			1.37 (0.55)	1.18 (0.84)	1.55 (0.42)
	+B, Tl			3.35 (0.51)	5.67 (0.84)	5.93 (0.69)
	+B, Ta			5.22 (1.37)	5.35 (0.17)	6.94 (1.40)
Ear	–B, Tl		ND		3.13 (1.51)	1.14 (0.53)
	–B, Ta				6.81 (1.12)	2.72 (1.80)
	+B, Tl				7.50 (1.32)	5.48 (0.81)
	+B, Ta				6.28 (0.48)	3.12 (0.24)

–B = 0 µM boron added, +B = 10 µM B added, Tl = low night temperature, Ta = ambient night temperature. The treatments of B supply and night temperature started at 31 days after transplanting when the eighth leaf was emerging. The eighth leaf was the youngest emerged blade at the start of treatment. The ninth leaf was the flag leaf. ND = not determined.

Table 3b. Statistical summary of effects of B supply and temperature treatments on B concentrations in the eighth and ninth leaves and the ears in wheat plants (cv. SW 41) for selected days after starting the treatment (DAST). The values are mean squares. Levels of significance are * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$

Source of variation		df	1 DAST	3 DAST	7 DAST	12 DAST	18 DAST
Eighth leaf	B supply	1	1.9	32.7***	50.0***	128.6***	8.5***
	Temperature	1	1.0	1.9*	11.2***	5.3*	0.0
	Interaction	1	2.4*	5.1**	7.5***	0.9	0.0
	Residual	12	0.5	0.3	0.3	0.7	0.3
Ninth leaf	B supply	1			39.3***	71.6***	104.8***
	Temperature	1			5.3*	0.3	2.2
	Interaction	1			2.1	0.0	0.3
	Residual	12			0.7	0.5	0.7
Ear	B supply	1				13.7**	22.5***
	Temperature	1				5.6	0.6
	Interaction	1				22.2**	14.5**
	Residual	12				1.4	1.1

Table 4. Potassium leakage (µg K^+ per g fresh weight over 2 hours) out of the youngest emerged leaf blades of wheat (cv. SW 41) for selected days after starting the treatment (DAST). Plants were subjected to a factorial combination of temperature and B supply treatments at the reproductive stage. The values are means of four replicates, followed by standard deviation in the parentheses. Mean squares are shown together with levels of significance: * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$

	Treatment	1 DAST	3 DAST	7 DAST	12 DAST	18 DAST
	–B, Tl	227 (38)	230 (24)	246 (49)	187 (12)	170 (15)
	–B, Ta	185 (18)	295 (53)	194 (64)	189 (23)	206 (22)
	+B, Tl	199 (22)	236 (17)	329 (90)	177 (25)	205 (34)
	+B, Ta	159 (24)	254 (15)	210 (26)	164 (17)	174 (13)
Source of variation	df					
B supply	1	2948	1246	9555	1228	9
Temperature	1	6765 **	6988 *	29223 *	138	17
Interaction	1	2	2266	4523	204	4506 *
Residual	12	720	989	3837	397	518

–B = 0 µM boron added, +B = 10 µM B added, Tl = low night temperature, Ta = ambient night temperature. The treatments of B supply and night temperature started 31 days after transplanting when the eighth leaf was emerging. At 1 and 3 DAST, the youngest emerging blades (YEB) were the eighth leaves; at 7, 12 and 18 DAST, the YEB were the ninth leaves.

Table 5. Elongation rate (cm/day) of the ninth leaf blade of wheat (cv. SW 41) for selected days after starting the treatment (DAST). Plants were subjected to a factorial combination of temperature and B supply treatments at reproductive stage. The values are means of four replicates, followed by standard deviation in the parentheses. Mean squares are shown together with levels of significance: * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$

	Treatment	5–6 DAST	6–7 DAST	7–8 DAST	8–10 DAST
	–B, Tl	4.4 (0.47)	3.9 (0.32)	3.7 (0.40)	6.6 (1.09)
	–B, Ta	5.3 (0.14)	4.5 (0.27)	4.0 (0.92)	5.2 (0.96)
	+B, Tl	4.4 (0.32)	4.1 (0.52)	3.6 (0.24)	6.0 (0.49)
	+B, Ta	5.8 (1.34)	4.2 (0.35)	3.9 (0.30)	5.8 (0.39)
Source of variation	df				
B supply	1	0.23	0.03	0.02	0.0
Temperature	1	5.57 **	0.50	0.36	2.9
Interaction NS					

Table 6. Boron concentrations (mg/kg dry matter) in the youngest emerged blades of wheat (cv. Wilgoyne) for selected days after starting the treatment (DAST). Plants were subjected to a factorial combination of temperature and B supply treatments at the vegetative stage. The values are means of four replicates, followed by standard deviation in parentheses. Mean squares are shown together with levels of significance: * = $P \le 0.05$, ** = $P \le 0.01$, *** = $P \le 0.001$

	Treatment	0 DAST	3 DAST	6 DAST	9 DAST	12 DAST
	–B, Tl	2.05 (0.19)	0.93 (0.17)	0.54 (0.14)	0.85 (0.23)	0.89 (0.61)
	–B, Ta	2.05 (0.19)	1.74 (0.18)	0.68 (0.34)	1.01 (0.47)	1.26 (0.44)
	+B, Tl	2.63 (0.21)	3.05 (0.43)	3.55 (0.31)	4.33 (0.39)	4.07 (0.43)
	+B, Ta	2.63 (0.21)	3.60 (0.70)	4.14 (0.65)	5.45 (1.06)	4.36 (0.14)
Source of variation	df					
B supply	1	1.2***	13.5***	35.8***	57.2***	36.4***
Temperature	1	0.0	1.6*	0.4	1.6	0.4
Interaction NS						

–B = 0 µM boron added, +B = 10 µM B added, Tl = low night temperature, Ta = ambient night temperature. The treatments of B supply and night temperature started 26 days after transplanting, when the seventh leaves were emerging.

Table 7. Potassium leakage (µg K^+ per g fresh weight over 2 hours) out of the youngest emerged leaf blades of wheat (cv. Wilgoyne) for selected days after starting the treatment (DAST). Plants were subjected to a factorial combination of temperature and B supply treatments at the reproductive stage. The values are means of four replicates, followed by standard deviation in parentheses. Mean squares are shown together with levels of significance: * = $P \le 0.05$, ** = $P \le 0.01$, *** = $P \le 0.001$

	Treatment	0 DAST	3 DAST	6 DAST	9 DAST	12 DAST
	–B, Tl	249 (81)	277 (147)	218 (35)	335 (206)	270 (75)
	–B, Ta	249 (81)	334 (273)	412 (70)	268 (57)	273 (58)
	+B, Tl	240 (31)	346 (157)	260 (70)	257 (80)	274 (63)
	+B, Ta	240 (31)	429 (316)	224 (27)	309 (71)	251 (26)
Source of variation	df					
B supply	1	306	26732	21462 *	1388	342
Temperature	1	0	19600	24806 *	189	420
Interaction	1	0	729	52900 **	14221	676
Residual	12	3794	55491	2962	14273	3401

–B = 0 µM boron added, +B = 10 µM B added, Tl = low night temperature, Ta = ambient night temperature. The treatments of B supply and night temperature started 26 days after transplanting, when the seventh leaf was emerging.

Table 8. Elongation rate (cm/day) of the seventh leaf blade of wheat (cv. Wilgoyne) for selected days after starting treatment (DAST). Plants were subjected to a factorial combination of temperature and B supply treatments at the vegetative stage. The values are means of four replicates, followed by standard deviation in parentheses. Mean squares are shown together with levels of significance: * = $P \leq 0.05$, ** = $P \leq 0.01$, *** = $P \leq 0.001$

	Treatment	1–2 DAST	2–3 DAST	3–4 DAST	4–5 DAST	5–6 DAST
	–B, Tl	4.8 (1.45)	4.3 (0.96)	3.9 (0.40)	8.5 (0.28)	3.5 (0.64)
	–B, Ta	5.4 (0.45)	4.5 (0.69)	5.2 (0.80)	7.9 (0.40)	2.7 (0.32)
	+B, Tl	5.6 (1.03)	3.7 (0.46)	4.8 (0.60)	9.2 (0.45)	4.0 (0.33)
	+B, Ta	6.1 (1.99)	5.2 (0.30)	5.0 (0.34)	8.4 (0.62)	2.4 (1.07)
Source of variation	df					
B supply	1	2.4	0.0	0.4	1.4*	0.0
Temperature	1	1.3	2.7*	2.2*	1.9**	6.0**
Interaction NS						

Table 9. Effects of B supply and night temperature treatments for 18 days on the grain set index in wheat plants (cv. SW 41). The values are means of four replicates, followed by standard errors in parentheses

Treatment	CMU %	LAC %
–B, Tl	52.6 (18.2)	53.5 (14.4)
–B, Ta	6.8 (4.6)	19.3 (5.6)
+B, Tl	94.4 (3.0)	81.4 (4.8)
+B, Ta	95.2 (2.5)	80.4 (9.0)

–B = 0 μM boron added, +B = 10 μM B added, Tl = low night temperature, Ta = ambient night temperature. CMU % is defined as the percentage of grain-set florets out of the central 20 florets of an ear (the method devised and used at Chiang Mai University); LAC % is defined as the percentage of grain-set florets out of the total number of florets of an ear (the method used by Lumle Agricultural Research Centre).

In contrast to the responses of leaf blades, spikelet fertility and grain set index were significantly decreased by the –B treatment in the present study. A similar result was also observed in the study by Rerkasem et al. (1993). These effects of B deficiency are attributed to poor pollen viability at low B supply and possibly to low B in the stigma and style of the floret (Cheng and Rerkasem 1993). The depression in grain set index in plants at low night temperature was associated with leaf B concentrations of 1 to 2 mg/kg and with ear concentrations of 1 mg/kg. In contrast, in plants at ambient night temperature, similar concentrations of leaf B were associated with substantially lower grain set index. Moreover, B concentrations in the ears at 12 and 18 DAT were actually higher in the plants at ambient temperatures than those at low night temperature, whereas grain set index was markedly lower. However, clearly, ear B concentrations of more than 3 mg/kg were adequate for grain set whereas concentrations of less than this at 18 DAT were associated with marked decreases in grain set index.

Low night temperature did not enhance the effects of the –B treatment on leaf blade elongation and K leakage from YEB in plants at vegetative and reproductive stages in the present experiment. It significantly delayed the development of plants at the reproductive stage, however, resulting in about six days' delay in anthesis of the main stems. As a result, the +B plants at low night temperature had fewer florets per spikelet than those at ambient night temperature.

The results suggest that the timing of B supply to the florets is crucial for the development of the reproductive parts and eventual fertilisation. There was a higher spikelet fertility and grain set index in the –B plants at low night temperature than those at ambient temperature. A part of the developmental process of ear and pollen in the –B plants at low night temperature might have coincided

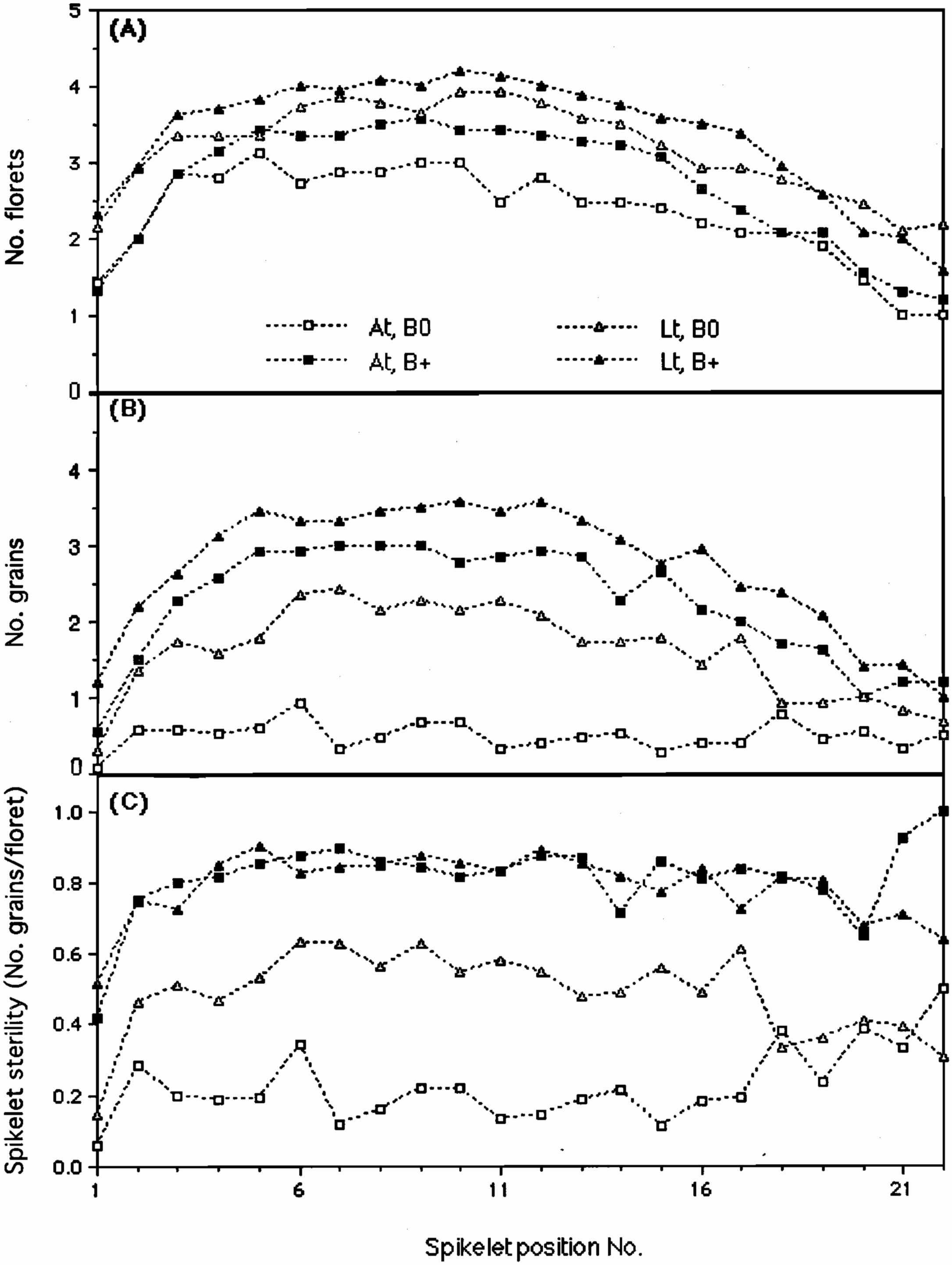

Figure 2. Effects of B supply and night temperature treatments on (A) number of florets per spikelet, (B) number of grain per spikelet and (C) spikelet fertility (number of grains per floret) in wheat plants (cv. SW 41) grown in the glasshouse. Tl = low night temperature; Ta = ambient night temperature, B0 = 0 μM B added, B+ = 10 μM B added.

with the resupply of B at the end of the treatment period (18 days after starting treatment). It is important to identify the critical stage of reproductive development when B deficiency causes irreversible damage to the fertility of florets. This knowledge can provide a basis for the correct timing of foliar B fertilisation to minimise the probability of grain set failure in wheat.

In conclusion, the results from the present study further confirmed the low internal B requirement for the vegetative growth of wheat plants. There was a distinct difference in sensitivity to B withdrawal between vegetative and reproductive parts of the same plant. This difference could be caused by the differences in external or internal B requirements, or both.

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Country review papers and ideas papers

Wheat Sterility in Bangladesh: an Overview of the Problem, Research and Possible Solutions

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Abstract

Years of observations of sterility in Bangladesh growers' wheat fields and intensive research have shown that the causes of sterility are many-factored. Low soil boron concentrations had been hypothesised to be the major cause, but data did not support this assumption. Probable causes include low light caused by foggy weather, low temperatures over many days during wheat flowering, and saturated or waterlogged soil. These factors affect transpiration, which in turn affects the uptake of boron from the soil during the critical preflowering or flowering period. Research results are summarised. New or unproven hypotheses are formulated.

LARGE-SCALE wheat production began in Bangladesh in the late 1970s. It expanded over the next decade but has since become fairly constant at around 700 000 ha. There are many reasons for this stagnation in production. The foremost factor is the changing of wheat land in the 1980s to winter rice and the consequent previously fallow marginal lands being brought into wheat cultivation. Scientists have noted sterility in wheat for many years in Bangladesh, mostly coming from genotypes prone to sterility, which were discarded. Since the mid 1980s, widespread sterility has been observed in growers' fields in some areas of Bangladesh but only in some years. Since then, a great deal of research data has been generated. Although the causes have been hypothesised and are now better understood, prevention of sterility in growers' fields remains elusive.

Researchers have induced sterility in pot trials and in research plots by shading, waterlogging or fogging, but have not reproduced the same type or symptoms of sterility that occur in the growers' fields.

Observations in Growers' Fields

What does sterility look like when it occurs in growers' fields? In early March 1993, we were a part of a survey that went throughout northern and north-western Bangladesh to investigate the many reports from extension officers of sterility in the growers' wheat fields. We viewed more than 100 plots exhibiting sterility. We saw a blackening of the leaves, culms and spikes. These blackened ears often exhibited 100% sterility. Accompanying pathologists confirmed that the blackening was due to secondary fungal infections. Non-sterile plots and plants in the same fields did not exhibit this. The secondary infection was probably due to the accumulation of carbohydrates in the leaves, stem and spikes near physiological maturity because there was nowhere for them to go.

Growers told us that many of these sterile fields had been irrigated. Close to 90% of them said that water stood in their fields after irrigation because of a concurrent rainfall. Inspection of the fields showed that sterility occurred in the depressed areas. There was no sterility on higher ground.

Although shading has been shown to induce sterility under research conditions, wheat growing under trees did not express any more sterility than wheat in full sun. One 0.5 ha field in full sun was completely sterile except one 2 m^2 plot in the middle. This plot was part of a larger area where water had been standing. However, the grower said that the small plot was where he had buried his buffalo the previous season. Probably an increase in both fertility and organic matter content of the small plot saved it from sterility.

One of us (Saifuzzaman) has studied the weather patterns during the wheat-growing season since sterility was first observed in growers' fields in the mid 1980s. I have been able to show convincingly that foggy weather (high humidity), low temperatures and sometimes rainfall during or

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before flowering were prevalent during the years when sterility occurred (that is, 1987, 1989, 1990 and 1993). No sterility has been found in years when there is little foggy weather or rainfall, despite cooler temperatures (for example, 1995).

Although many of the fields with sterile crops we have observed have been waterlogged, the soils in these regions are generally acidic silty sands. How can such soils, with high hydraulic conductivities, become waterlogged? In 1993 there were hard, driving rains after the growers weeded but before they gave their last irrigation. Such rains would cause a crust, which could have caused waterlogging after the last irrigation at flowering. Some of these soils have a distinct hard pan at 10 to 15 cm that also can contribute to waterlogging.

We also visited four of the Wheat Research Centre's (WRC) varietal demonstrations on growers' plots in those areas where extension officers had reported severe sterility. Each site's grower indicated there had been standing water at one time during the growing cycle. In each case, however, Sonalika showed no sterility whereas the other three lines showed variable amounts of sterility. Probably Sonalika flowered before the other three, and before the waterlogging, thus escaping sterility. In visits made before the 1993 incidence of sterility in growers' fields, we made similar observations but saw less waterlogging. One grower's field had staggered planting dates but the same variety and crop management. Only one planting date exhibited severe sterility; the other had none.

Many soil samples from growers' fields were taken over many years and wheat was planted in the same soil in pots. None has ever reproduced the sterility symptoms. Although some soils had low boron concentrations, others were adequate.

Sunflower is considered an indicator crop for many nutrient deficiencies, and especially boron. One project has placed thousands of sunflower demonstrations in the northern region of Dinajpur for more than four years, yet none has been reported to exhibit sterility. However, chickpea and mustard have exhibited sterility in these soils. Mustard showed a response to applied boron by increased fertility of the pods. Even early transplanted winter rice and late transplanted summer rice have shown sterility in north-western and northern Bangladesh owing to cooler weather during the reproductive stage (Haque et al. 1992).

The WRC has planted crossing blocks of various lines collected throughout the world at four sowing dates at many of its research stations. Observations of complete genotypic sterility have been made of some lines, but only at some of the sowing dates. Later plantings tend to have less sterility than the same lines at earlier plantings.

What have we been able to conclude about the causes of sterility in growers' fields from our observations?

- In years where widespread sterility occurs, more foggy weather and associated rainfall had occurred during or before flowering.
- When sterility occurs, it is usually severe, reducing yields by 25% to 100%.
- Secondary infection occurs near physiological maturity, causing a blackening of the plants by sporulating bodies.
- Some sort of waterlogging occurred right before or near flowering in some fields.
- All plots showing sterility had lighter-textured soils.
- Some event occurred at flowering that caused some varieties to go sterile.
- In depressed areas of the fields, sterility was more frequent.
- Fertilizers applied in the sterile fields were used at generally lower than normal or recommended rates.
- Evidence exists to show that low soil B concentrations alone are not the reason for sterility.

Research Results

The WRC began a literature search when sterility was first observed in fields. The literature is full of information on sterility in wheat, but most data are induced from experiments, not deduced from tests in growers' fields. Although there is no doubt that boron has an influence on sterility in the soils in South Asia, the data produced in Bangladesh are very inconclusive about boron. Whereas some researchers from the Bangladesh Agricultural University have documented yield increases with soil applications of boron (Jahuruddin 1991), no one has shown that the yield response was due to less sterility. Foliar sprays with boron have also been inconclusive (Badruzaman 1995; Jahuruddin 1991).

We know that boron is essentially immobile in the plant, travelling only little in the phloem, and mostly being taken up with water in the transpiration stream of the xylem as H_3BO_3. The anion,

$B(OH)_4^-$, is formed only at high pH and would be adsorbed by sesquioxides and clay minerals in the soil and by polysaccharides in the cell walls of plants (Mengel and Kirby 1982). Critical concentrations of soil boron are highly dependent on:

- organic matter (OM) content (low OM contents mean lower B amounts)
- potassium content (high K amounts mean higher B availability)
- pH (the lower the pH, the higher B availability)
- phosphorus concentrations (high concentrations of P mean lower B availability).

In Bangladesh, the OM level is generally at or below 1% in those soils prone to sterility. The soil potassium concentrations are lower than a decade ago and will continue to become lower owing to crop intensification, potassium 'mining' and the growers not applying potash. These lighter soils are acidic and have generally low phosphorus concentrations. Thus some of the predispositions to low boron concentrations exist under Bangladesh conditions, but not others.

Various trials have been conducted under waterlogged conditions at the WRC to see if this condition alone could produce sterility, and if so, if there is genetic variability breeders could use to prevent sterility. Lines from CIMMYT and many national and international nurseries have been grown under waterlogging. Some lines have been identified as more tolerant under Bangladesh conditions. However, the sterility that had been observed in some years in growers' fields has not been replicated in this experiment so far.

Plant boron concentrations depend on the tissue: concentrations are higher in lower plant parts and lower in higher plant parts. Boron concentrations vary even among plant parts, with anthers, stigmas and ovaries having twice the concentrations in stems (Mengel and Kirby 1982). Despite soil applications of boron and double the uptake of boron in the flag leaves or young spikes, the incidence of sterility has not been affected under high humidity and low light (Saifuzzaman, unpublished data). There were no differences in the incidence of sterility in soils with higher and lower than critical concentrations of boron (Saifuzzaman 1994). How can we corroborate the fact that despite not having low boron concen-trations in the soil, we still observe sterility in growers' fields? Some conclusions from Saifuzzaman's Ph.D. dissertation on wheat sterility include:

- Soil boron alone at any concentration has not induced sterility in any experiment conducted in Bangladesh.
- Even with applied boron, high humidity and shading still cause sterility.
- There was no decrease in sterility incidence when boron was added to the soil.
- Low light caused by fog at low temperatures (< 6°C) and the consequent high humidity probably contribute more to farmers' field sterility than low soil boron concentrations (based on shading, humidity and temperature studies in the field).
- There are genotypic differences in response to sterility but the explanations for these differences remain elusive.

Solutions Are Evasive

As there have been no conclusive data produced in Bangladesh to show that the application of boron to the soil or plant reduces or prevents sterility, what can we recommend to growers? Although no results suggest a solution, from years of observations of wheat sterility in Bangladesh, some solutions can be proposed:

- Low organic matter, low boron concentrations and low boron availability generally occur concurrently. Addition of organic matter can increase boron concentrations and reduce the risk of crusting, which can cause waterlogging. Also, the benefits of OM to soil structure and root growth are well documented. The On-Farm Research Division of the Bangladesh Agriculture Research Institute has many research sites in northern Bangladesh for which it makes and annually applies compost at the full recommended rate. These fields have never exhibited sterility, despite growers' plots nearby having sterility. The WRC recommends farmyard manure (FYM) at 5 to 10 t/ha for optimum wheat production. In 1990 surveys, growers were using this amount. Recent surveys, however, indicate an average rate of 3 to 4 t FYM for those applying it, and indicate that half apply none (Meisner 1992, 1995). With rising fuel demand, FYM availability and its application to the soil will continue to decline as the manure is used in rural communities as a cooking fuel.
- Low fertility produces poor root systems. This can impair uptake of boron and other nutrients

under normal conditions. Uptake is much less under waterlogged or other stressed conditions. Maintaining medium- to high-level fertility in the soil to promote good root and shoot growth makes sense, given the intensification of cropping in Bangladesh.

- Staggered planting dates can be used to avoid the risk of environmental conditions that might cause sterility.
- Develop stress-tolerant genotypes. Some studies have indicated that more efficient micronutrient uptake and the ability of a plant to develop various rooting patterns are linked with tolerance to waterlogging (van Ginkel, CIMMYT, unpublished data). Thus waterlogging could be a useful screening tool.
- Control irrigation such that it is not concurrent with wheat flowering, eliminating the potential for waterlogging as a possible cause of sterility.

Hypotheses to Test

Temperature effects on pollen formation and sterility have not been fully dealt with. Although air temperature is an indicator of overall upper soil and plant canopy temperatures, on a micro-scale the temperature at the anther level might be lower than that of the canopy or air. Fog alone cannot cause the sterility in growers' field, as sterility occurs only in depressions. Waterlogging was repeatedly mentioned by growers in 1993. Thus there are multiple factors within the air and soil that are causing the sterility in the fields. One hypothesis is that the fog creates the cool temperature, low light and high humidity during the time when pollen formation occurs, reducing the transpiration stream and reducing the boron uptake during that time. Thus low soil boron concentrations concurrent with the lack of uptake caused by low transpiration might be the main cause, even though each alone is not. Others speculate that the high humidity alone with condensation on the spikes and leaves could either hinder pollination or allow a localised pathogen. Another hypothesis is that thrips, which are also present in many sterile fields, are a cause.

As boron's involvement in carbohydrate assimilation is well known in the literature, low light caused by fog plus impaired uptake of boron caused by low transpiration rate might explain sterility in wheat. No one has tested this hypothesis to our knowledge.

Are there any other stress conditions that we have not considered that predispose wheat to sterility? Although we have documented waterlogging as sometimes being associated with sterility, other water stresses occur during the growing season in Bangladesh that perhaps no one has considered.

More work is needed on genotypic differences in tolerance to waterlogging, low light and high humidity, and efficiency in boron uptake. Preliminary work by the WRC indicates there is genetic variability in all these factors. Already it has begun to introduce such lines into its breeding programs.

Conclusions

Many years of research in many countries in South and Southeast Asia have eliminated single factors as the main causes of wheat sterility in growers' fields. Low soil boron concentrations were thought to be the main factor, though data in Bangladesh do not support the hypothesis. Genotypic differences are obvious, but more work is needed to assess and understand them. In Bangladesh, low light caused by foggy weather under low temperatures for several days before or during flowering under low soil boron conditions is the probable cause of sterility in growers' fields. Prevention of sterility by better crop management is possible by increasing the soil OM levels, which improve the soil structure for better rooting as well as increasing nutrient availability and reducing the risk of waterlogging.

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Summary of Wheat Sterility Research in Nepal

S. P. Pandey*

Abstract

Wheat sterility in Nepal was first observed in 1964–65. Since then it has been increasingly reported, mainly from the eastern, central and western Terai. Yield losses have been as high as 95%. Cases have also been observed in the foothills as well as the high altitude areas of the eastern, central and western developmental regions. Factors linked with sterility include low or high temperature; dry and hot winds or abrupt change of weather conditions at the flowering period; nutrient deficiencies, particularly nitrogen and boron; genetic or varietal factors; thrips sucking the pollen; and moisture excess or stress at the flowering stage. The inconsistent and irregular trend of sterility occurrence indicates that different factors are responsible in different environments. It is suggested that the problem can be solved by the identification, evaluation and breeding of sterility-tolerant varieties.

Record of the Occurrence of Wheat Sterility

Wheat sterility was first observed in Nepal in 1964–65, in the Indian NP (New Pusa) series of cultivars in the Sunsari, Morang and Jhapa districts of the eastern Terai, when wheat cultivation was first introduced to the area (Joshy 1976). This created a hue and cry among the participating farmers and puzzled a team of multidisciplinary agriculturists from Kathmandu.

Since then, the occurrence of wheat sterility has been increasingly reported, mainly from the eastern, central and western Terai up to the Rupandehi district (Bhattarai 1973, 1974, 1975, 1976, 1977, 1978; Pandey 1979; Rana 1980, 1983, 1984; Panth 1981; Giri 1985). A number of cases have also been observed in the foothills and Lekh (high altitude) areas of the eastern, central and western developmental regions (Thapa and Russell 1980; Sthapit et al. 1987; Subedi et al. 1995). Grain yield losses have been as high as 95%.

Varieties NL-30 and HD-1982, which were released by the National Wheat Development Programme, failed in the eastern Terai because of severe sterility. Many other currently recommended varieties, except the short-duration ones (RR-21, NL-297), are still being affected by this problem.

Symptoms of Wheat Sterility

In the eastern Terai, the symptom of wheat sterility appears a few days after anthesis as pale green, translucent and loose spikelets with open glumes. If the florets in such a spikelet are examined, the anthers look light yellow but shrunken. They remain enclosed within the lemma and palea and show no further elongation of the filament. The pistil looks well developed, with swollen lodicules and two prominent feathery stigmata. If all the florets in the spike are sterile, the ear and straw eventually become watery and blackish.

Hypothesis for Why Wheat Sterility Occurs

After the inception of the National Wheat Development Programme in 1972, a number of field trials were conducted to identify the causes of sterility. Researchers are still confused by the strange nature of its occurrence, however. Different views, speculations and findings have been proposed for the possible causes of the problem, including:

- low or high temperature, dry and hot wind or abrupt change of weather at flowering
- nutrient deficiencies, particularly nitrogen and boron
- genetic or varietal factors
- thrips sucking the pollen
- moisture excess or deficit at flowering.

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Plant Nutrition and Wheat Sterility

In 1974, I reported that wheat sterility might not be due to micronutrient deficiency (including boron) under Tarahara and Bhairahawa farm conditions (Pandey 1974). Later, I concluded that fertilising with nitrogen at 100 kg/ha significantly reduced both floret and spike sterility in Jupateco-73, S-227 and HD-1982, irrespective of seeding date (Pandey 1977). However, the early maturing variety RR-21 had no sterility even when nitrogen was not supplied.

Sthapit (1988) found that the application of borax at 15 kg/ha reduced sterility by 28% in Tarahara and 8% in Khairanitar, but that there was no effect in Lumle and Pakhribas. Similar but inconsistent results were reported recently by Subedi et al. (1995), though they were inclined to conclude that boron deficiency and cool temperatures are the most likely causes of wheat sterility in Nepal.

Moisture Stresses

Mishra et al. (1992) and I (Pandey 1979) observed severe wheat sterility under conditions of excess moisture and poor drainage at Tarahara, as well as on several farmers' fields in the eastern Terai. Sthapit (1988), in contrast, reported that wheat sterility that was caused mainly by boron deficiency was further compounded by dry conditions.

Ecological Variability

Wheat sterility has occurred in diversified agro-climatic zones: in the Terai (tropical); in the Tars, valleys and terraces of the mid hills (subtropical); and in the Lekh (temperate). I have no knowledge, however, of its occurrence in any ecological zones of the mid- and far-western developmental region, which is the main traditional wheat-growing area in Nepal.

Genotype Diversity

In all previous studies, marked genotypic differences were a common observation. Late maturing varieties were found to be more prone to sterility than early maturing ones in tropical and subtropical climates (Pandey 1977, 1979; Mishra, pers. comm.). In contrast, early maturing varieties were found to be more vulnerable in a temperate climate (Bimb and Sthapit 1987). Sterility-susceptible and -tolerant wheat genotypes were observed for conditions of low nitrogen (Pandey 1977) or low boron nutrition (Subedi et al. 1995), moisture excess (Mishra et al. 1992) or moisture stress (Sthapit 1988), and low or high temperature regimes (Subedi et al. 1995).

Future Research Priorities for Overcoming Wheat Sterility

The inconsistent and irregular occurrence of sterility indicates that different factors are responsible in different environments. Therefore, to further our understanding, we need to :

- verify that nitrogen and boron nutrition are causal and identify the factors, such as temperature, humidity, moisture stress, drainage, and nutrient interactions and antagonism, that might be affecting their availability in the sterility-prone areas
- identify and evaluate the environmental factors (temperature, humidity, foggy weather, hot and dry winds) and winter requirements for growing non-sterile wheat
- compare ecological differences (Nepalgunj v. Bhairahwa/Tarahara and Lumle/Pakhribas v. Jumla) under similar plant nutrition and water stress
- define the role of nitrogen and boron nutrition in reproduction mechanisms through plant physiological studies

The identification, evaluation and breeding of sterility-tolerant varieties are likely to be the solution to the problem.

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Review of Research into Wheat Sterility: the Experience of Pakhribas Agricultural Centre

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Abstract

Wheat (*Triticum aestivum* L.) is a major cereal in Nepal. It is grown in diverse agroclimatic conditions. Several varieties have been released commercially for different domains, but a satisfactory level of production has not been achieved so far. This is due mainly to several production constraints, of which sterility is one of the most important. Sterility is defined as the loss of generative power of male or female organs or both.

Six experiments were carried out to identify the possible cause of sterility. Fertilizers (chemicals plus compost and compost alone), boron, sowing times, genotypes, growing conditions (greenhouse, partially greenhouse and field) and temperature (duration of cool injury) were examined during the period 1978 to 1992. Some genotypes are more susceptible to conditions that could cause sterility than others. Environment has an even greater role in causing sterility. Boron applications did not reduce sterility. The effect sof these factors on pollen and ovules need to be further investigated.

STERILITY is the loss of generative power of either male or female flowers or both. Sterility in wheat is common in Nepal. This problem was first reported at Pakhribas Agricultural Centre (PAC) in 1977–78 (Tiwari 1991) and has remained one of the major problems in wheat in the PAC region. It appears irrespective of genotype and year, although some genotypes are less affected than others. Scientists involved in wheat research have reported that losses could vary from 25% to 90% (Sthapit et al. 1989). But at PAC in bad years (1988–89 and 1994–95), the loss was even higher in some of the early maturing genotypes.

When PAC noticed this problem in 1977–78, it started working on the identification of possible causes. Since then, alone and in collaboration with the Wheat Research Programme and Lumle Agricultural Research Centre, it has conducted six trials between 1978 and 1992. The identification of possible causes of sterility in wheat was the common objective of those trials. Environmental, genetic and other factors (fertilizers, compost, some micronutrients and planting dates) were examined. Those trials revealed that both environment and genotype had an effect on sterility in wheat, though we have concluded that the environment has a greater role in causing sterility than genetic factors.

Literature on wheat sterility suggests that it can be caused by several factors. These include environmental stresses during flowering, such as cold injury (Euthumiades 1981; Marcellos and Single 1984; Kim et al. 1985; Prescott et al. 1986), water stress or drought (Bingham 1966; Saini et al. 1984); high temperature just before anthesis (Warrington et al. 1977; Rawson and Bagga 1979; Saini et al. 1984); deficiency of micronutrients in the soil, such as copper (Graham 1975), boron (Simojoki 1972; Singh et al. 1976; Lu, quoted by Sthapit et al. 1989) and manganese (Sharma 1992); plant hormones such as abscisic acid (Morgan 1980); and low light intensity between floret initiation and anthesis (Willey and Holliday 1971; Allan 1987).

Materials and Methods

In 1978–79, three factors, namely sowing date, variety and fertilizers, were evaluated at two PAC sites (PAC North Farm, 1850 m, and South Farm, 1450 m a.s.l.). Three then-popular varieties, RR-21 (Sonalika), Lerma-52 and Jupateco-73, were sown on eight different sowing dates, from 3 September to 10 November 1978 at ten-day intervals. There were two fertilizer treatments, chemical fertilizers (60 kg N/ha and 30 kg P/ha) plus compost at 15 t/ha, and compost only at 15 t/ha (Table 1).

In 1980–81, RR-21 was evaluated with three boron treatments, borax 10 kg/ha, boric acid

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10 kg/ha and a control (Table 2). In 1981–82, it was evaluated with and without boron at six planting dates, from 20 September to 9 November 1981 at ten-day intervals (Table 3). All these experiments were laid out as randomised complete block designs.

The same trial was repeated in 1987–88 and 1988–89. Three factors (planting date, variety and boron) were evaluated. There were two planting dates (2 November and 1 December in 1987 and 25 October and 25 November in 1988), three varieties (RR-21, NL-460 (Annapurna-3) and Triveni), and two rates of borax (0 and 15 kg/ha) (Table 4). Sterility was assessed by grasping individual ears between finger and thumb and drawing the hand up the ear from base to tip. This is a very superficial method of estimating sterility and depends mainly on practical experience and expertise.

During this period it became clear that a controlled environment was required to assess the factors more precisely. Controlled environment studies were consequently carried out in 1991–92 in England. Three varieties, two from Nepal, namely Sonalika (RR-21) and Annapurna-3 (before release called NL-460), and one from Europe, Axona, were evaluated in three environments. Sonalika is early maturing, has a medium height, and is adapted to a wide range of agroclimatic conditions. These days, however, it seems to be more prone to sterility in Nepal. Annapurna-3 is medium maturing, has fairly good tillering, and is smaller than Sonalika. It is supposed to be less prone to sterility and is adapted to the mid altitudes of Nepal (1000 to 1700 m). Both have an erect growth habit. Axona is a European spring wheat, characterised by a prostrate to semi-erect growth habit, a medium straw length, and high tillering. Two experiments were carried out simultaneously. In the first experiment the three varieties were evaluated in three environments:

- greenhouse, where wheat plants were grown throughout (G1)
- partially greenhouse, where plants were grown in the greenhouse up to about 35 days then transferred to an open field (G2)
- field, where plants were grown throughout (G3).

In the second experiment, the same varieties were subjected to cold injury for various durations during anthesis. The main objective of this experiment was to see the effect on sterility of cold temperature (1°C ± 0.5) for various durations (control, 1 hour, 6 hours and 24 hours) during anthesis.

To estimate sterility, individual florets in each spike were counted and total fertile and sterile florets were recorded. Sterility percentage was calculated by using the following formula:

$$\text{sterility (\%)} = \frac{a-b}{a} \times 100$$

where a = total numbers of florets per spike and b = total florets that set grains.

This is tedious but gives an accurate figure. Observations were taken when grains were clearly visible. Spikelets, excluding the basal vestigial ones, were counted. Percentage fertility of each floret was determined by numbering florets in each spikelet. The floret on the rachilla closest to the rachis was designated 1 and florets progressively further from the rachis were designated serially 2, 3, 4, 5 and 6.

Results and Discussion

In 1978–79, fertilizer did not have a significant effect on sterility. The percentage sterility of RR-21, Lerma-52 and Jupateco-73 was 12%, 6% and 10% under compost and 9%, 7% and 11% under chemical fertilizers plus compost (Table 1). Crops planted on 10 and 20 October with compost and on 10 September and 10 October with chemical fertilizers plus compost suffered relatively more sterility, irrespective of genotype. There was no consistency in the severity of sterility due to sowing dates, however. These dates might have coincided with cool temperatures during anthesis. It seems that Lerma-52 was affected least by sterility, irrespective of fertilizers or sowing dates. This suggests that both environment and genetic factors are responsible for sterility.

In 1980, RR-21 was evaluated with three boron treatments (10 kg borax, 10 kg boric acid and control) because boron deficiency was suspected as one of the causes of sterility in wheat. Contradictorily, boron application produced more sterility than the control, though there was a slight yield advantage in the plus boron treatments (Table 2).

In 1981, RR-21 was evaluated with and without boron at six planting dates (Table 3). October plantings suffered much more from sterility than earlier and later plantings. This finding supports the results of the 1978–79 trial. Boron application

Table 1. Sterility (%) and grain yield (kg/ha) for different wheat varieties at different sowing dates, 1978–79

	Sowing date	RR-21		Lerma-52		Jupateco-73		Mean	
		sterility	yield	sterility	yield	sterility	yield	sterility	yield
Compost only (mean of two sites)									
1	3 Sep.	12	1875	7	1698	12	2870	10	2148
2	10 Sep.	8	2063	7	3110	11	2391	8	2521
3	20 Sep.	13	3704	6	1912	8	2339	9	2651
4	1 Oct.	10	2146	6	3422	12	2427	9	2665
5	10 Oct.	15	2688	7	2375	13	2448	11	2504
6	20 Oct.	20	1756	4	2427	12	2782	12	2321
7	30 Oct.	9	1156	3	1839	9	1380	7	1458
8	10 Nov.	8	1427	5	1651	4	1829	6	1636
	Mean	12	2102	6	2304	10	2308	9	2238
Compost + chemical fertilizer (mean of two sites)									
1	3 Sep.	6	3526	6	2906	9	3052	7	3161
2	10 Sep.	10	3177	8	3469	13	4240	10	3629
3	20 Sep.	8	3531	7	3328	13	3901	9	3587
4	1 Oct.	6	3980	6	2318	4	3855	5	3384
5	10 Oct.	14	2766	11	2464	15	2568	13	2599
6	20 Oct.	8	2756	5	3203	14	2157	9	2705
7	30 Oct.	13	2297	4	2370	11	1469	9	2045
8	10 Nov.	8	1177	5	1761	5	1886	6	1608
	Mean	9	2901	7	2727	11	2891	9	2840

reduced sterility by only 2% compared with the control plot (Table 3).

The same trial was repeated for two consecutive years (1987–88 and 1988–89). Three factors, planting date, variety and boron, were evaluated. Overall, sterility was less in the first year than in the second year (5.07% v. 27.3%). Most of the genotypes grown on the North Farm (1850 m) suffered in 1988–89 and the same might have happened in this experiment also. There was no remarkable difference in sterility due to the application of boron, but there was a significant effect of sowing date in the second year. The 25 November sowing suffered more from sterility than the 25 October sowing (34% v. 21%) (Table 4). This contradicts the findings of the previous study that October-planted crops suffered more. This is not surprising because the temperature trend fluctuates over the years (Gurung and Resham 1992).

The severity of sterility was high in all genotypes in the second year. Combining results for both years indicates that Annapurna-3 suffered the least sterility (12.6%). There was no specific indication of a boron requirement in the genotype, though there was some influence of sowing time on sterility. The severity was less in early plantings in both years. A similar though minor trend was seen in Triveni.

Table 2. Sterility (%) and grain yield (kg/ha) of RR-21 in three boron treatments, 1980

Treatments	Sterility %	Yield (kg/ha)
Borax 10 kg/ha	21	1890
Boric acid 10 kg/ha	16	1770
Control	15	1710

Table 3. Effects of boron and sowing date on wheat sterility (%) and yield (kg/ha) in 1981–82

	20 Sep.		30 Sep.		10 Oct.		20 Oct.		30 Oct.		9 Nov.		Mean	
B	%	kg/ha	%	kg/ha	%	kg/ha	%	kg/ha	%	kg/ha	%	kg/ha	%	kg/ha
0	20	2013	32	1561	35	919	44	956	37	1111	37	1517	33	1346
10	12	2349	29	1763	31	1382	44	1017	35	1176	32	1115	31	1467
Mean	16	2181	31	1662	33	1151	44	987	36	1144	35	1316	32	1406

Boron	NS	Time of sowing	**
CV%	35	LSD 1%	8
		CV%	26
		Interaction	NS

NS = not significant. ** = significant at $P < 0.01$.
CV = coefficient of variation

In 1991–92, a further experiment was conducted in England to evaluate the effects of different environments on sterility in Nepalese and Axona wheats. RR-21 (Sonalika) had the highest floret sterility (41%), which was significantly greater ($P < 0.001$) than Annapurna-3 (30%) and Axona (30%). Similarly, greenhouse and greenhouse-to-field wheat produced the highest sterility (37% and 35%), whereas field-grown plants were less sterile (27%) (Table 5). Fertility of florets was not uniform but decreased with distance from the rachis (Fig. 1). Visual observations and manually grasping individual heads indicated that later tillers suffered more from sterility than early tillers. This was particularly evident in later tillers of RR-21. In some cases late tillers had 100% sterility (Tiwari 1992).

General Discussion and Conclusion

As reported by several scientists, and confirmed in the current studies, sterility in wheat is not unusual but the degree of incidence varies between varieties and environments. For example, Annapurna-3 seems to be more tolerant than RR-21 (Tables 4 and 5). This supports observations of genotypic variation by Asaad (1985), Law et al. (1985), Gale and Youssefian (1985) and Singh (1985, pers. comm.). This observation was also made at PAC in on-station varietal research. For example, in one trial, two genotypes, NL-712 and NL-714, were allocated to adjacent plots (by randomisation) in two replications out of three, and the genotypes averaged respectively 65% and 9% sterility (Tiwari and Rijal 1995). So even in the same environment some genotypes are more vulnerable than others. RR-21 is always found to suffer the most sterility, irrespective of growing environment. This further supports the notion that there is considerable genotypic variation in ability to achieve fertility. Facultative lines (spring × winter) have shown more resistance than others. Different genotypes could have special climatic requirements for specific stages. Consequently,

Table 4. Sterility (%) due to variety and borax (kg/ha) over two years (1987–88 and 1988–89)

Sowing	2 Nov. 87		1 Dec. 87		25 Oct. 88		25 Nov. 88		Mean
Borax	0	15	0	15	0	15	0	15	
RR-21	5	8	6	5	37	37	33	32	21.4
NL-460	3	2	5	5	7	9	34	36	12.6
Triveni	6	3	5	8	22	14	27	40	15.6
Means									
Borax	4.7	4.3	5.3	6	22	20	31	36	
Date	4.5		5.6		21		33.6		
Year	5.1				27.3				

Table 5. Sterility (%) due to variety, environment and interaction (1991–92)

Variety	Floret count			Mean
	Greenhouse only	Greenhouse then field	Field only	
RR-21	44	47	31	41
Annapurna-3	32	33	26	30
Axona	36	28	26	30
Mean	37	35	27	

Growing condition **	Variety **
SED = 1.57	SED = 0.748

SED = standard error of difference

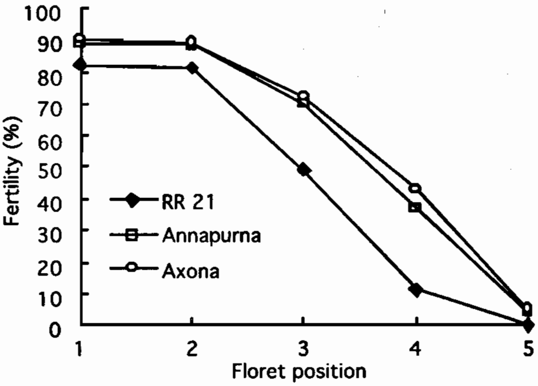

Figure 1. Percentage fertility in each floret position in three varieties of wheat (Tiwari 1992)

any abnormal fluctuation in climate, particularly during anthesis, could cause failure in fertilisation, which would lead to low or no grain set.

The application of fertilizers (Table 1) and boron (Tables 3 and 4) did not diminish the occurrence of sterility in PAC conditions. In some years, boron application actually increased the severity of sterility (Table 4). This result is at variance with the findings of Sthapit et al. (1989) and Galrao and Sousa (1988). The level of requirement for micronutrients in any plant is critical, and slight deviations from that level can be detrimental. Soil was not analysed before the PAC experiments (one of the weak points of this research), so the basal levels of boron in the soil were not known. It is possible that the PAC experimental sites might not have been deficient in boron and therefore there was no boron response. The rates used (10 kg/ha in 1981–82 and 15 kg/ha in 1987–88 and 1988–89) could have been excessive.

Similarly, though wheat is adapted to a wide range of environments, sterility can vary between environments, as the research presented here has shown. This is possible because reproductive tissues of the developing wheat ear are extremely susceptible to even small fluctuations in, for example, temperature and relative humidity, when the conditions are close to the extreme range. Therefore, wheat grown at the different dates and conditions used in this research might have resulted in the occasional coincidence of anthesis with abnormal environments, thus changing the incidence of sterility. The research done in 1991–92 also clearly indicated the effect of genotype and growing environments in causing wheat sterility (Table 5). Annapurna-3 was found to be better than the other two varieties. Similarly, fieldgrown wheat was less sterile than greenhouse-grown wheat.

The duration of cool temperature treatment had no effect on sterility. Suspected reasons are that one hour of injury might be sufficient to produce sterility comparable to that of longer durations because the fertilisation period in any crop is short. In the control greenhouse treatment, the temperature in the greenhouse was relatively high during anthesis, which could have reduced pollen viability, thus resulting in sterility comparable to that of the cool temperature treatments (Tiwari 1992). This notion is possible because both high and low temperatures can cause sterility in wheat (Toda 1972a,b,c; Warrington et al. 1977; Rawson and Bagga 1979; Boese 1987; Ledent et al. 1988; Tashiro and Wardlaw 1990).

In this regard, Evans et al. (1975) have stated that high temperature during the period from 15 days before to 5 days after anthesis reduces the number of grains per spike. Ledent et al. (1988) stated that temperature below 5°C at pollen meiosis could be responsible for low seed setting. This might be one of the reasons why in 1988 (Khadka 1989) and in 1994–95 (Tiwari and Rijal 1995) most of the genotypes in the varietal trial at PAC suffered more than 90% sterility. But the problem used to occur in some measure every year. January and February are the coldest months and have some frost each year that generally coincides with the flowering period of wheat (Table 6). Therefore this might be one of the reasons why there are sterility problems at PAC every year.

Summarising these research experiences, it can be concluded that variety, growing environment and their possible interactions are factors contributing to sterility in wheat. Boron application did not reduce sterility, suggesting that boron inadequacy is not the cause of sterility in PAC conditions. It can also be said that a single factor alone might not be fully responsible for causing sterility. Rather, it could be a result of several factors that might have interacted with the environment.

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Table 6. Weather data at PAC averaged from 1975 to 1994

Month	Air temp. °C		Grass temp. °C
	Maximum	Minimum	Minimum
Sep.	22.8	16.1	15
Oct.	21.7	12.8	10.4
Nov.	18.9	9.4	7.9
Dec.	15.7	6.3	1.5
Jan.	14.4	4.8	0.7
Feb.	16.1	6.2	2.9
Mar.	20.0	9.8	6.1

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Overview of Wheat Sterility Problem and Research Findings To Date in the Western Hills of Nepal

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Abstract

This paper assesses the extent of wheat sterility in the western hills of Nepal and reviews what have been perceived as its causes. The sterility problem has been increasingly observed in both the irrigated rice–wheat system and the maize–wheat system in the uplands. The extent of losses has been as high as 98%.

Though the problem is considered to be caused by several environmental factors in various combinations, the two most important factors identified have been low available boron and low temperature during the flowering period. Boron availability is thought to be modified by factors such as water stress, alkalinity and low nutrition, especially nitrogen.

Considerable variation exists between genotypes in their tolerance to boron deficiency and cool temperatures. No genotypes have yet been identified that tolerate both. Genotypes tolerant to cool temperatures are highly susceptible to boron deficiency and vice versa. Research is required to define what level of low temperature causes sterility, and to determine the degree of interaction between the various factors that affect boron availability.

A comparison of grain-set pattern in normal and partially sterile spikes revealed that the numbers of grains in the basal and middle thirds of a spike were similar, but the number in the top third was almost half that in the basal and middle portions.

WHEAT (*Triticum aestivum* L.) is the third most important cereal crop in Nepal after rice and maize. It is cultivated on about 634 000 ha and yields on average 1.41 t/ha (MOF 1994). Distribution of wheat by area is 51% in the terai, 42% in the hills and 7% in the mountains (ASD 1992). In Lumle Agricultural Research Centre's (LARC) Research Command Area (RCA), in eight hill districts of the western hills of Nepal, the estimated area of wheat is about 39 000 ha, with an average productivity of 1.41 t/ha. Between 1980–81 and 1991–92, the area and productivity of wheat in the RCA have been increased by 102% and 35% respectively.

The first report of wheat sterility being a serious problem in Nepal was from the eastern terai (Sunsari, Morang and Jhapa districts) in 1964, when improved, high-yielding Mexican wheats were first made available to farmers (Mishra et al. 1992). Since then, other workers (NWDP 1977; Rana 1980; Sthapit 1988; Sthapit et al. 1989; Subedi et al. 1992, 1993; Subedi 1993; Subedi and Budhathoki 1995a) have reported wheat sterility as a problem in other parts of Nepal. The problem is becoming increasingly important in LARC's RCA under both the rice–wheat system in khet lands and the maize–wheat system in bari lands. Research work on this problem was started at LARC in 1987. Studies on various aspects of the problem continue. LARC is the leading centre in Nepal for research into this problem.

This report describes the nature and extent of wheat sterility in Nepal with special reference to the RCA of LARC, and discusses the perceived causes of the problem and the research results achieved so far.

Extent of the Problem

The extent of the problem in Nepal has been estimated at various research stations, in farmers' fields, and in experimental plots. So far, the problem has been reported from the Sunsari, Morang, Jhapa, Chitwan, Lamjung, Gorkha, Tanahun, Kaski, Palpa, Bhaktapur, Rupandehi and Dhankuta (Pakhribas Agricultural Centre) districts of Nepal.

Systematic surveys to estimate the extent of the problem were carried out in the 1993, 1994 and 1995 winter seasons at LARC and in selected problem areas within LARC's RCA. A summary of these survey findings is presented in Table 1.

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These surveys showed that the extent of the problem varies between years and that it is even more serious and widespread than previously assumed. The surveys also found that because of the severity of the problem, some farmers had abandoned wheat harvests.

Possible Causes and Research Accomplishments

Since 1987, LARC has been involved in research to understand the possible causes of and solutions to the wheat sterility problem. Research has shown that sterility can be caused by many factors of the environment and by these factors in various combinations.

Boron (B) deficiency has been well established as a cause of wheat sterility (Singh et al. 1976; Li et al. 1978; Liu et al. 1981; Rerkasem et al. 1989; Sthapit 1988; Sthapit et al. 1989; Subedi et al. 1993). Boron is an essential micronutrient for normal growth and development of plants. It plays a crucial role in fertilisation in higher plants: anthers appear to be particularly sensitive to B deficiency (Vasil 1963). Cheng and Rerkasem (1992) found that in B-deficient wheat, the pollen does not accumulate starch, and the nuclei, when present, are abnormal. Rerkasem (1993) found that the fertility of both male and female parts of the wheat florets appears to be affected by B deficiency. Subedi et al. (1993) found that there was a significant reduction in percentage sterility with the application of boron and that there was also a highly significant boron × genotype interaction (Fig. 1). However, when they repeated the same experiment in the following year, they found far less sterility (15.3% compared with 41.2%) and the effect of boron was less. To further complicate the issue, they found that there was no significant effect of boron in an experiment using five boron rates (0, 0.5, 1.0, 1.5, 2.0 kg/ha) in three problem areas over two seasons (1993–94 and 1994–95).

Sowing time also had a significant effect on sterility in a low hill rice–wheat system. In a sowing date × genotype × boron experiment carried out at Rishing Patan (420 m) during the winter of 1994–95, sterility was significantly increased when the crop was planted on 21 December compared with 21 November and 6 December. Grain yield of wheat was also significantly reduced in the later sown crop. There was also a significant effect of boron on sterility.

How much boron is needed by wheat plants at key crop stages, the critical soil concentrations of boron, and uptake rates required are not clear. In China, grain set failure was reported to occur at soil B concentrations of between 0.18 and 0.52 ppm (Li et al. 1978). Soils having less than 0.50 ppm B are assumed to be boron deficient (Liu et al. 1981). In Thailand, Rerkasem et al. (1989) found reduced grain set in soils with less than 0.15 ppm hot-water-soluble B, and found different responses between genotypes. Katyal and Friesen (1987) reported that if hot-water-soluble B in a soil is less than 0.30 ppm, B deficiency can be suspected. In Nepal, however, sterility has been

Table 1. The extent of the sterility problem with soil analysis information in selected problem areas in LARC's Research Command Area in 1993, 1994 and 1995 (After Subedi et al. (1993), Subedi and Budhathoki (1995a) and Subedi et al. (1995))

Location (altitude)	Cropping system	Sterility %			Soil information (mean)		
		1993	1994	1995	pH	Total N %	Avail. B (ppm)
LARC (1675 m)	Maize–wheat	15–65	16–69	11–96	5.3	0.44	0.10
Khairenitar (480 m)	Maize–wheat	37–100	21–98	24–93	7.8	0.09	0.38
Rishing Patan (400 m)	Rice–wheat	45–96	15–43	18–61	7.7	0.15	0.50
Banjakhet (1000 m)	Rice–wheat	59–90	21–35	28–34	5.7	0.12	0.42
Bhusundi Phant (500 m)	Rice–wheat	49	49–71	23–38	6.3	0.09	0.30
Batulechour (1000 m)	Rice–wheat	46–66	24–91	35–55	6.5	0.09	0.70
Kharanephant (750 m)	Rice–wheat	30–92	20–43	39–62	7.4	0.18	0.36
Yampaphant (450 m)	Rice–wheat	–	–	33–51	6.8	0.18	0.52

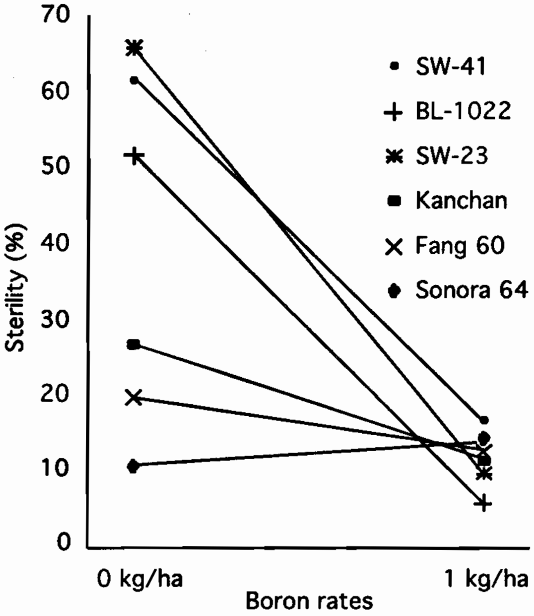

Figure 1. Effect of boron on percentage sterility of six genotypes of wheat at Khairanitar (480 m), 1992–93 (after Subedi et al. 1993)

observed in soils having up to 0.70 ppm B (Table 1).

Seasonal and within-plot variability of sterility shows that boron availability must be affected by other external factors. Drought, waterlogging (poor drainage), alkalinity and low nitrogen have been reported to be important factors affecting boron availability (Liu et al. 1981; Yang 1992; Subedi et al. 1993). The lowest boron contents are in acidic leached soils, coarse sandy soils and organic soils (Thompson and Troeh 1979). Katyal and Friesen (1987) also reported that boron is less available at high pH, perhaps due to calcium antagonism (alkalic calcareous soils). The findings of Subedi et al. (1993) are consistent with these results: more sterility was observed in calcareous soils with high pH (> 7). Pant and Rerkasem (1994) found that irrigation where B has been added enhanced grain set per spikelet in both susceptible and tolerant genotypes.

Cold stress is considered to be the other major factor that causes sterility in the middle and high hills (above 1400 m) in Nepal (Sthapit et al. 1989; Subedi 1993; Subedi et al. 1993). Frosts and snow at high altitudes cause both mechanical and physiological damage. Winter wheat can survive temperatures as low as –30°C, usually with snow cover, but spring wheats cannot survive cold winters (Haldone et al. 1982). All varieties grown in Nepal are spring types. The coincidence of their flowering time with the coolest winter weather in January and February) means that no wheat variety grown at high altitude can escape being affected. Evans et al. (1975), citing Hoshikawa, report that the optimum temperature for fertilisation of wheat is 18° to 24°C, the minimum is 10°C and maximum is 32°C. In LARC conditions, however, night temperatures drop to –1°C or even lower in January and February, which is the flowering period of the October-sown wheat.

Research at LARC in the past few years has shown that low temperatures between heading and flowering (anthesis) affect grain set. In an experimental crop grown between heading and maturity in an unheated glasshouse, sterility was 8% less in 1993 and 14% less in 1994 than in a crop grown in an open field. There was also an interaction between genotype and location (Fig. 2).

Similarly, a genotype × sowing time experiment carried out at Lumle for two years (1993 and 1994) showed that the crops sown on 11 and 18 October suffered more than crops sown later (Fig. 3). There was also considerable genotypic and seasonal variation in sterility. Two types of genotypic difference were observed. One was probably an escape mechanism, in which later flowering of some genotypes allowed them to avoid the coolest period. The other was probably cold tolerance in some genotypes at flowering. Despite our concentrated efforts in the field at Lumle, we could not establish the critical low temperature that causes sterility or the developmental stage of wheat that is most critical at low temperature.

No single variety has been found to be suitable for both boron-deficient and cool temperature areas. Varieties susceptible to cold were tolerant to boron and vice versa. Some varieties, such as NL-297, Lerma-52 and BL-1249, were intermediate types that had moderate sterility under both conditions. Some of the contrasting genotypes for cool weather and boron deficiency are listed in Table 2.

At Lumle (1675 m), cool temperature is the problem. At Khairanitar (480 m), boron deficiency is the problem, but the amount of available boron has increased owing to boron applications over several years. As a result, the level of sterility has reduced dramatically.

Most of the cold-tolerant genotypes were highly susceptible to boron deficiency. For example, varieties such as Annapurna-1, Annapurna-2, Annapurna-3, BL-1022, Triveni and BL-1135 had very high sterility at Khairanitar (boron-deficient conditions) in the 1992–93 and 1993–94 seasons, and very low sterility at Lumle.

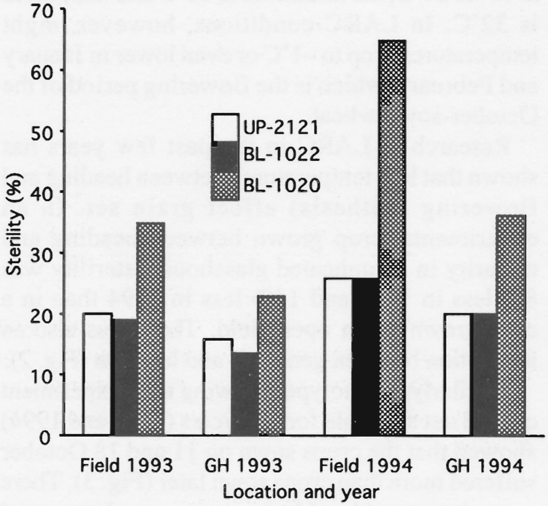

Figure 2. Effect of temperature on the percentage sterility of three genotypes of wheat in glasshouse and open field in 1992–93 and 1993–94 at Lumle (1675 m) (after Subedi et al. 1993 and Subedi and Budhathoki 1995a)

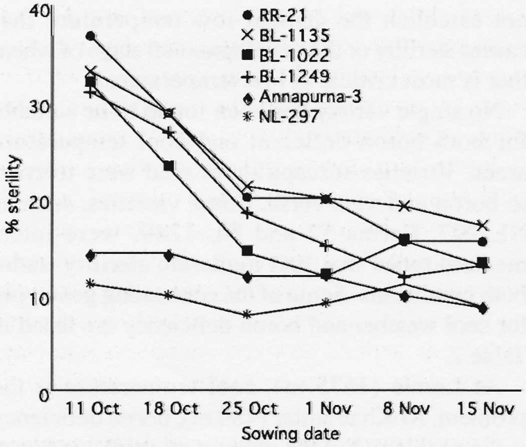

Figure 3. Effect of sowing time on the percentage sterility of six wheat genotypes at Lumle (1675 m) (mean of 1992–93 and 1993–94) (after: Subedi and Budhathoki 1995b)

High temperature does not cause grain set failure in Nepal. Wheat is grown in winter and flowering is completed before temperatures rise. (Late planting in the terai part of Nepal could result in shrivelled grains because of the high temperatures and dry air during the grainfilling period.) But high humidity could be a factor causing sterility in Nepal. During winter, high humidity and fogs occur frequently in the river basin areas, where the problem of sterility is high.

Water deficits have been reported by many workers as a cause of grain set failure in wheat. Seed set in wheat is very susceptible to water stress (Evans et al. 1975). Saini and Aspinall (1982) found that the proportion of apparently normal florets that produced grains was reduced when water deficits occurred during and immediately after meiosis of the generative tissues. A large proportion of the anthers on water-stressed plants were small and shrivelled, did not dehisce normally, and contained pollen that was devoid of normal cytoplasmic constituents and showed no staining reaction with triphenyl tetrazolium chloride (TTC). Water stress also affects boron uptake, as the rate of transpiration greatly affects boron transport into leaves and its distribution between plant parts. Pant and Rerkasem (1994) also found that irrigation with boron-containing water enhanced grain set irrespective of genotype. This problem of water stress can be experienced in Nepal, particularly under rain-fed and late-sown conditions.

A pot experiment carried out at Lumle to study the effects of water stress and flooding showed that water stress (induced by withholding water) during the period between flag leaf ligule visible (FLLV) and anthesis resulted in stunted plants, burning of lower leaves, the production of excessive numbers of late tillers, shorter spikes, and ultimately less grain set and reduced grain size (Table 3).

Waterlogging as a cause of sterility was reported by Mishra et al. (1992) in low-lying and poorer-drained areas of Tarahara Farm in Nepal, whereas higher and better drained plots showed no problem at all. Similarly, Subedi et al. (1993) also observed more sterility in low-lying wet areas and along irrigation canals. Yang (1992) also observed more sterility in sites that have lower, damp and badly drained soils. The pot experiments described above, however, did not show the effect of waterlogging. Flooding at various stages of the wheat crop caused

Table 2. Sterility of different wheat genotypes in cool temperature (Lumle) and boron-deficient (Khairanitar) conditions (after Subedi et al. (1993), Subedi and Budhathoki (1995a) and Subedi et al (1995))

Variety	Sterility %					
	Khairenitar (480 m)			Lumle (1675 m)		
	1993	1994	1995	1993	1994	1995
Annapurna-1	96.7	79.8	8.1	21.1	19.2	20.7
Annapurna-2	96.0	83.6	28.0	22.2	23.4	17.2
Annapurna-3	94.7	58.9	18.1	21.8	19.3	17.2
Lerma-52	51.2	27.1	20.9	14.4	25.4	11.1
NL-297	16.2	35.6	29.9	20.7	29.3	19.3
BL-1022	58.5	71.7	18.5	21.8	23.9	31.3
BL-1135	54.6	86.2	31.1	27.7	40.8	–
BL-1249	19.6	32.6	15.5	17.4	28.1	24.1
RR-21	35.5	38.1	9.9	17.5	35.7	32.7
Triveni	57.7	50.5	26.0	19.4	19.3	35.9

a favourable effect on many of the variables measured (Subedi et al. 1995). The mechanism by which waterlogging causes wheat sterility is not understood, but it is thought that waterlogging might act by reducing boron availability.

Mishra et al. (1992) and Subedi et al. (1993) reported that sterility was observed more in low nitrogen soils. In a fertility trial on wheat at Yampaphant, Subedi and Gurung (1995) found that the use of chemical fertilizer (NPK) significantly reduced sterility compared with no NPK.

A preliminary study was carried out at Rishing Patan during the winter season of 1995 to understand the grain set pattern in partial spikes. This showed that in normal spikes, the grain set pattern was similar in the bottom and middle part of the spike, but that there were fewer grains in the top part. In the partial spikes, the grain numbers were also similar in the basal and middle portion of the spike, but were reduced to almost half in the upper part (Fig. 4).

A similar study was carried out at Lumle to see whether the completely gaping glumes observed after heading set any grains. Ten completely gaped and transparent spikes were randomly tagged and the grain set pattern was studied at maturity. This showed that even the spikes with all glumes gaping set at least some grains. However, the number of grains set in the top position of the spike was quite low (Fig. 5).

In summary, boron deficiency and cool temperatures are the two most important factors causing wheat sterility in Nepal. Factors such as water stress, waterlogging, alkalinity and low nitrogen are also associated with boron availability, but there are still many unanswered questions relating to the importance of interactions between all the factors.

Conclusion

Wheat sterility is becoming an important limitation to wheat production in Nepal by causing severe yield losses. There are various factors causing sterility, among which boron deficiency, cool temperatures from heading to anthesis and water stress at FLLV stage are foremost. However, the critical low temperature that causes sterility is not known, the developmental stage of wheat that is most sensitive to cool temperature has not been defined, and the mechanism of cool-temperature-induced sterility (that is, the reproductive physiology of cold-stressed-wheat) is not understood.

Boron deficiency as a factor causing sterility is well established, but the availability of boron is influenced by several other factors, such as moisture stress, waterlogging, alkalinity and lower nitrogen in the soil. Further studies are needed to understand the mechanisms involved. Examination of the interactions between the factors and ways by which boron can be made more available is also required.

It is now evident that genotypes differ considerably in their ability to be fertile under conditions of low boron. It is not known, however, whether some genotypes take up more boron than others or indeed whether genotypes differ in their

Table 3. Effect of flooding and water stress at different stages on yield components and grain set of wheat at Lumle, 1995 (After Subedi et al. 1995)

Treatments	Plant height (cm)	Tillers per plant	Late tillers per plant	Spike length (cm)	Sterility (%)	1000 seed weight (g)
Control (no stress)	78.8	3.2	0.45	9.6	14.6	53.4
Water withheld 61–70 DAS*	77.0	3.1	0.40	10.0	19.4	50.5
Water withheld 71–80 DAS	82.3	3.3	0.73	9.9	20.8	53.1
Water withheld 81–90 DAS	77.8	4.1	1.10	10.3	20.6	44.1
Water withheld 91–100 DAS	73.0	3.5	0.98	8.6	35.4	57.0
Water withheld 101–110 DAS	66.3	5.6	3.0	9.9	34.7	44.2
Water withheld 111–120 DAS	79.5	2.9	0.58	9.1	18.3	39.6
Flooded 61–70 DAS	86.5	2.7	0.15	9.9	13.7	62.6
Flooded 71–80 DAS	83.8	2.7	0.20	10.1	20.6	60.7
Flooded 81–90 DAS	86.5	3.1	0.33	10.3	17.7	47.5
Flooded 91–100 DAS	81.3	3.2	0.45	9.9	14.5	47.6
Flooded 101–110 DAS	79.5	3.7	0.58	10.4	15.4	49.1
Flooded 111–120 DAS	79.3	3.1	0.75	9.7	16.4	50.3
Mean	79.3	3.4	0.74	9.8	20.2	50.7
SED	1.73	0.30	0.19	0.28	5.76	3.28
P	0.000	0.000	0.000	0.000	0.006	0.000

* DAS = days after sowing

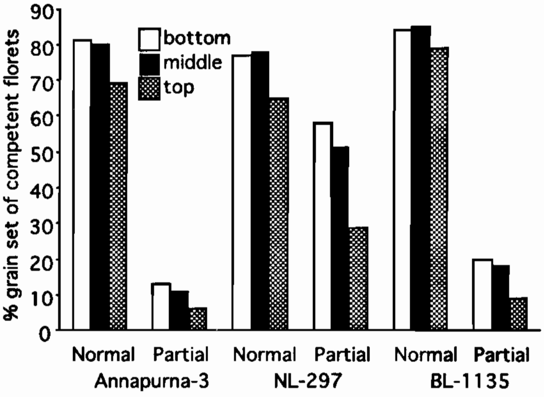

Figure 4. Grain set pattern of normal and partial spikes of three genotypes of wheat at Rishing Patan, 1995

propensity for setting grains with equivalent boron uptake. This aspect is an important avenue for future research.

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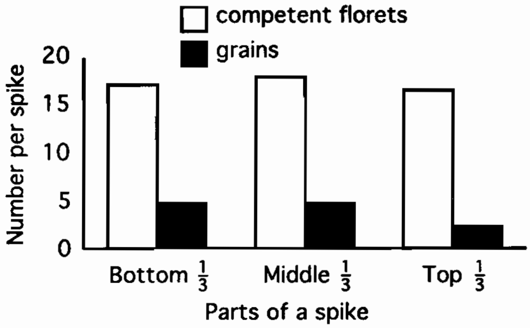

Figure 5. Grain set pattern in the completely transparent and gaping spikes at Lumle, 1995

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Wheat Research in Nepal: Efforts and Achievements

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Abstract

In Nepal, the extensive cultivation of improved wheat varieties started soon after the introduction of the Mexican semi-dwarf wheat varieties during the mid 1960s. Since the establishment of the National Wheat Development Programme in 1972, wheat research has been more systematic, strategic and meaningful. Efforts made in wheat research and major achievements to date are discussed in brief.

ALTHOUGH wheat has been cultivated in Nepal from time immemorial, extensive cultivation of improved varieties is recent. Until the early 1960s, wheat cultivation was limited to hill areas in the mid and far western regions. The area sown to tall traditional varieties and total production were minimal (Fig. 1). However, soon after the introduction of the Mexican semi-dwarf wheats from India during the mid 1960s, several improved varieties such as Pitic-62, LR-64, Kalyansona and RR-21 (Sonalika) were released. This marked the end of the era of traditional wheat varieties in the country. There began a big jump in both area and total production of wheat. RR-21 proved outstanding because of its adaptation to a wide range of environments and agroecological zones extending from the terai to mid and high hills. It was a predominant variety of the 1970s and early 1980s and remains a popular variety in the hills, despite its susceptibility to major diseases.

Since the inception of the then National Wheat Development Programme (NWDP) in 1972, wheat research in Nepal has become more systematic, strategic and meaningful. It has been further strengthened with the establishment of a new autonomous institution called the Nepal Agriculture Research Council (NARC) in 1990. In the process of reorganising the NARC, the former NWDP has been renamed the National Wheat Research Programme (NWRP).

Major Efforts in Wheat Research: Past and Present

Wheat research has focused on three important areas: crop improvement, agronomy and soil fertility, and outreach. From the very beginning, the crop improvement program has had high priority and remains the main activity of NWRP .

Crop improvement

A review of wheat research in crop improvement shows that the main focus in the 1970s and early 1980s was on the evaluation and selection of disease-resistant and high yielding bread wheat genotypes, mostly introduced from international institutions like CIMMYT and ICARDA, and from countries like India and the USA. In addition to bread wheat, a small program in triticale varietal improvement was also begun. However, the poor grain quality and late maturity of triticale genotypes (Shakya 1979, 1980) discouraged triticale research.

A hybridisation program, begun soon after the inception of NWDP, was not very effective, mainly because of the lack of identified sources of resistance. However, F_2 populations introduced directly from CIMMYT were more useful to the program. Shuttling the selected progenies between Bhairahwa (105 m a.s.l.) and Nigale (2500 m) further provided the opportunity of advancing two generations a year under two contrasting environments. BL-1022, a recently released variety, is the outcome of such a scheme. Screening a large number of genotypes against major diseases under natural and artificial conditions and then selecting the best ones has effectively minimised epidemics.

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Since the inception of NARC, there has been a change in priorities and approaches. Research is now oriented more towards the production environments. Four wheat production environments have been identified in the terai, tars and lower valleys (TTL) up to 1000 m altitude and the mid and high hills (MHH) above 1000 m altitude. Crop improvement activities aiming to develop suitable wheat varieties for these environments are currently organised under four specific project headings:

Varietal development for TTL: timely sowing and irrigated (TS/I) conditions

- Hybridisation and segregating generations
- Advanced lines
- International bread wheat screening nursery from CIMMYT
- International spring wheat yield nursery from CIMMYT
- Elite selection wheat yield trial from CIMMYT
- Advanced varietal trial (TS/I) from India
- Initial evaluation trial (TS/I)
- Coordinated varietal trial (TS/I)

Varietal development for TTL: timely sowing and rainfed (TS/R) conditions

- Hybridisation and segregating generations
- Rainfed nursery
- Semi-arid wheat screening nursery from CIMMYT
- Semi-arid wheat yield trial from CIMMYT
- Advanced varietal trial (TS/R) from India
- Initial evaluation trial (TS/R)
- Coordinated varietal trial (TS/R)

Varietal development for TTL: late sowing and irrigated (LS/I) conditions

- Hybridisation and segregating generations
- Advanced lines
- Warmer area wheat screening nursery from CIMMYT
- Heat-tolerant wheat yield trial from CIMMYT
- Advanced varietal trial (LS/I) from India

Varietal development for MHH: irrigated (khet) and rainfed (bari)

- Hybridisation and segregating generations
- Advanced lines
- Rainfed nursery
- Shuttle breeding (summer screening nurseries)
- International bread wheat screening nursery from CIMMYT
- Semi-arid wheat screening nursery from CIMMYT
- Advanced varietal trial hill (TS/I) from India
- Advanced varietal trial hill (TS/R) from India
- Advanced varietal trial hill (LS/R) from India
- Advanced varietal trial, high altitude, from India
- Initial evaluation trial
- Coordinated varietal trial

Breeding for resistance to major biotic and abiotic stresses has a high priority at present in the crop improvement program. Several stresses are known to affect the wheat crop directly or indirectly. The major diseases of national importance are foliar blight (*Helminthosporium* spp.) and leaf rust (*Puccinia recondita*) in the terai, and stripe rust (*P. striiformis*), leaf rust (*P. recondita*) and loose smut (*Ustilago tritici*) in the hills (Karna and Dongol 1981; Dongol 1982; Karki 1994; Devkota 1994). Therefore priority has been given to these diseases in breeding for resistance (Devkota et al. 1990; Devkota 1994). Breeding for tolerance to heat and drought stress is another area of high priority at present (Devkota 1994).

Wheat sterility has created highly localised problems. It has been reported regularly over the years with varying degrees of intensity from specific places including Tarahara (eastern terai), Pakhribas (eastern hills), Lumle (western hills) and Rampur (Chitwan Valley). Research in the past has aimed mainly at finding the causes of sterility. Review of the experimental results and experiences over the years suggest that the causes of wheat sterility are complex and that several factors are involved:

- Genotypes differ in performance. Nepal 297, RR-21, BL-1249, NL-298 are, to some extent, tolerant to sterility. BL-1022, UP-262, NL-30, on the other hand, are prone to sterility.
- Low nitrogen concentrations increase sterility (NWDP 1977a, b).
- Abrupt drops in temperature, particularly during anthesis, increase sterility.
- Excessive drought stress and excess water during anthesis increase sterility.
- Deficiency of micronutrients such as boron increases sterility.
- Continuous foggy weather for several days at anthesis causes sterility.

Lumle Agriculture Research Centre has the main responsibility for research work on wheat sterility. It collaborates closely with the NWRP and with other national and international institutions.

Agronomy and soil fertility

Past research into agronomy and soil fertility focused mainly on cultural, irrigation and fertility management. Most of the studies concerned with seeding date × variety, seeding date × N rate, variety × seed rate, variety × fertilizer, zero tillage and long-term fertility are still continuing.

With the establishment of NARC in 1990, more emphasis has been given to diagnostic surveys and regular monitoring in order to understand on-farm problems. Some of the major problems of wheat identified this way are late planting (when there is either excess or insufficient moisture), nutrient deficiencies (major elements such as N and P and possibly some micronutrients such as Zn, Bo, Mn), and poor initial stand establishment, particularly under the rice–wheat system. Wheat yield under the rice–wheat system is very low and declining, as shown by the results of long-term fertility experiments. As the area of wheat under the rice–wheat system in Nepal accounts for more than 80% of wheat production, current research into agronomy and soil fertility is designed mostly for dealing with the issues of long-term sustainability.

Outreach

One of the major outreach activities during the late 1970s and early 1980s was the 'minikit' program, run with the support of the Integrated Cereal Project. This program was very effective in two aspects: feedback about prerelease varieties and dissemination of recently released varieties. Farmers' field trials were another important activity. Farming system sites established at different places (including Pumdi Bhumdi, Chauri Jhari, Ratnanagar and Lele) had the responsibility for conducting these trials. In addition, agricultural development offices, farms, stations and non-government organisations were also actively involved in effective implementation of minikits and farmers' field trials.

There is now a change in the approach to outreach research. Farming system sites and the minikit program have ended, but several outreach research sites have been established in the command area of each outreach farm and station. All the on-farm research activities are conducted through these sites. Apart from the varietal farmers' field trials and preproduction verification trials, several other experiments on soil fertility and fertilizers and on weed, irrigation and cultural management are being conducted with the participation of cooperating farmers.

Achievements

Significant achievements from almost three decades of wheat research in Nepal can be measured in terms of varietal diversification, adoption of improved varieties, rate of yield gain, the tremendous increase in area and production of wheat, and returns to investment on wheat research.

Varietal diversification

The first Mexican semi-dwarf wheats were released in the late 1960s. Seventeen new cultivars of different genetic background have been released since the inception of NWDP in 1972. Thirteen of the 17 were released for the TTL production environments; the other four were released for the MHH environments.

Adoption of improved varieties

Farmers like stable varieties. A stable variety is judged by its capacity to perform well in a wide range of environments, despite biotic and abiotic stresses. Several of these varieties are currently under cultivation and have varying degrees of popularity (Table 1).

Annual rate of yield gain

The annual rate of genetic gain in wheat yields in Nepal from 1978 to 1990 was 1.25% (Morris et al. 1992). The potential for modern or improved varieties to increase productivity ranges from 0.5% to 2.0% a year (Byerlee 1994).

Increase in area and production of wheat

The first five genotypes listed in Table 1 contribute significantly to the area of cultivated wheat in Nepal. The overall effect of such diversified genotypes can be assessed from the tremendous expansion of the area sown to wheat and the simultaneous increase in production within the last three decades (Fig. 1). The area under improved varieties reached 90% of the total area sown to wheat by 1990 (CIMMYT 1993). Wheat area has increased from 118 000 ha in 1965–66 to 634 000 ha in

Table 1. Popular wheat varieties currently under cultivation in Nepal

Variety	Parentage	Year of release	Region	Production condition
UP-262	S308/Bajio 66	1978	TTL	TS/I
Triveni	HD1963/HD1931	1982	TTL	TS/I, TS/R
Nepal 297	HD2137/HD2186// HD2160	1985	TTL	TS/I, LS/I
Nepal 251	WH147/HD2160// WH147	1988	TTL	TS/I, TS/R
Annapurna-1	KVZ'S'/Buho// KAL/BB	1988	MHH	TS/I, PI
Annapurna-3	KVZ'S'/Buho// KAL/BB	1991	MHH	TS/I, PI, R (*bari*)
BL-1022	CM58794-1B-2B-5N-1B-OB	1991	W, MW, FW/TTL	TS/I, LS/I
BL-1135	QTZ/Tan	1994	TTL	TS/I, TS/R
Bhrikuti	Cont/COC75/3/ PLO//Fury/Ana	1994	TTL	TS/I, PI LS/I
Annapurna-4	KVZ/3/CC/Inia// CNO/Elgau/4/SN64	1994	MHH	TS/I, TS/R

TTL = terai, tars and lower valleys; MHH = mid and high hills; W = western region; MW = mid western region; FW = far western region; TS = timely sown; LS = late sown; I = irrigated; PI = partially irrigated; R = rainfed

1994–95. Simultaneously, total wheat production has grown from 157 000 t to 915 000 t.

Returns to wheat research

The returns to investment in wheat research in Nepal from 1960 to 1990 have been analysed. The internal rate of return calculated on the investment to wheat research as a whole is 75% and to wheat breeding only is 84% (Morris et al. 1992). This result is very encouraging and should be enough to justify future investment.

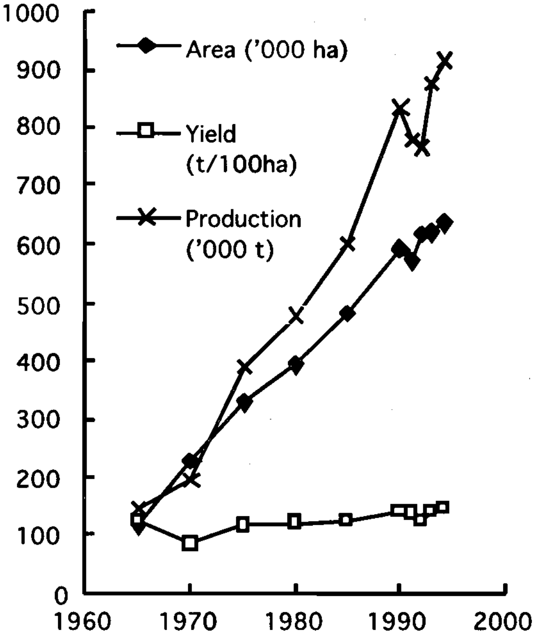

Figure 1. Increase in area, production and yield of wheat in Nepal, 1965–95

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Hypothesis for Why Sterility Occurs in Wheat in Asia

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Abstract

It is proposed that the primary cause of sterility in wheat in Asia is the inadequacy of boron moving into the generative zone during the 6 to 10 days of pollen formation. As boron movement is associated with transpiration, any component of the environment that changes transpiration flux at this time can play a part. Thus low available boron in the root zone will lead to sterility, particularly when coupled with low vapour pressure deficit, which limits transpiration, or with any environmental factor that limits stomatal opening (low radiation, water deficit or waterlogging). Increase in temperature can also increase sterility, though by a separate avenue: as the duration of the pollen formation process is modified by temperature, increased temperature will reduce the number of days during which the required boron can be acquired. Interplay between all these factors and their constantly changing magnitudes makes the problem appear to be one of considerable complexity, but, in fact, the causes are simple. It is proposed that pan evaporation during the phase of flag leaf emergence would be a good first order indicator of the probability of sterility occurring.

Factors that Might Be Involved in Causing Sterility

Many environmental variables have been linked with sterility:

- boron limitation (Rerkasem and Loneragan 1994)
- low radiation (cloudy dull weather, morning fogs, mists) (Willey and Holliday 1971, Saifuzzaman 1995)
- high humidity (Dawson and Wardlaw 1989)
- low humidity (Galrao and Sousa 1988)
- high temperature (Saini and Aspinall 1982)
- low temperature (Sthapit et al. 1989)
- drought or water shortage (Saini and Aspinall 1981)
- waterlogging or water excess (Misra et al. 1992)
- high pH (Bell and Dell 1995).

In short, it seems that almost all major environmental variables have been linked with sterility, though boron has received most attention. This paper begins by considering boron as the primary factor and the others as either modifiers of boron movement or contributors to sterility in their own right. Sterility has been variously defined, but for the purposes of this paper it is regarded as the absence of a grain in any floret that grows 'large enough' to contain a grain. 'Large enough' is judged as the minimum size of florets that do contain grains in 'normal' ears of the same genotype.

Some Facts about Boron

- Boron is required by the generative organs in relatively large concentrations. For example, anther concentrations can be up to six times those in the bulk ear (Rerkasem 1995).
- Boron is required continuously for cell wall development by the generative organs during their growth (Matoh et al. 1992).
- Boron probably moves into the roots passively, in association with water fluxes (Bell and Dell 1995).
- Boron moves within the plant almost exclusively in the transpiration stream (Kohl and Oertli 1961). Only minor amounts move in the phloem (Shelp 1987).
- Boron remobilisation between organs is minimal (Shorrocks 1991).

The consequence of these facts is that any restrictions in plant transpiration rate at any time during the generative stage could lead to incomplete development of the sexual organs through limiting boron movement. This would be accentuated in a plant growing in a soil with low boron availability.

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When is the Critical Stage for Damage Leading to Sterility in an Ear?

- The critical stage is after late double ridge and probably after terminal spikelet (B. Dell, pers. comm.).
- It occurs before anthesis (Dawson and Wardlaw 1989).
- It has been associated with pollen meiosis (Saini and Aspinall 1981, 1982), which approximates to the time of ligule emergence of the flag leaf (Dawson and Wardlaw 1989).

These facts suggest that the critical period possibly spans only 6 to 10 days, between emergence of the second-last leaf ligule and preheading.

The Hypothesis

Most sterility occurs as a result of environmental factors limiting the movement of water into and through the plant during the critical 6 to 10 days between emergence of the second-last leaf ligule and preheading and, by association, limiting the movement of boron into the generative regions.

Some Soil Factors Limiting Boron Uptake

- Low boron concentrations in the soil. Values of hot-water-soluble boron ranging between 0.12 and 0.38 mg/kg can result in sterility, but the degree depends on the location (Rerkasem et al. 1988; Li et al. quoted in Bell and Dell 1995).
- High pH, which prevents the roots from taking up the available boron (Bell and Dell 1995).
- The extent and efficiency of root exploration of the soil and when it occurs in relation to plant phenology.

The Environmental Factors Limiting Transpiration and Boron Uptake

- High humidity or, more correctly, low vapour pressure deficit (VPD). (See Rawson ('Parameters') in these Proceedings for a discussion of the calculation and meaning of VPD and its dependence on temperature.) Low VPD means that the air has limited capacity to accept water vapour from the plant's leaves, so transpiration could be low even though the stomata are open.
- Dew, fogs and mists. These make leaf-to-air VPD small, with the same consequence as high humidity.

Environmental Factors to Which the Plant Responds to Limit Transpiration through Stomatal Closure

- Low radiation, associated with cloud cover, mists and fogs or time of day, closes the stomata to a degree that depends on radiation level. This in turn reduces transpiration flux (see Rawson ('Parameters') in these Proceedings for magnitude of effects).
- Drought. Stomata close to conserve plant water.
- Low humidity. The effects of low humidity and drought are sometimes difficult to dissociate.
- High temperature. This can be associated with high VPD (see Rawson ('Parameters', Table 4) in these Proceedings for temperature and vapour pressure) and can lead to 'aerial drought' and stomatal closure in some species.
- Waterlogging. Stomata close in wheat (R. A. Richards, pers. comm.).
- Low soil temperature. Water cannot be conducted but stomata can close. This is probably a problem only in summer dicots and not in wheat.

A Special Effect of Temperature

Plant development rate increases linearly with increasing temperature (Slafer and Rawson 1994), so at higher temperature the critical period for 'sterilisation' is shortened. By corollary, there is less time for the uptake of boron. In the absence of increases in transpiration rate, for example, sterility is likely to be increased. Additionally, there will be less time for the plant to fix radiation for that critical phase, so less carbon will be available for organs growing and developing during the phase.

Conclusion

Commonly, there might be only two main factors associated with sterility—boron in the soil and transpiration during the critical phase—but these factors are driven by many variables. Although it might be quite difficult to guess from historical weather data the future likelihood of sterility occurring at any particular place, pan evaporation is a good simple indicator of transpiration potential by a crop. It integrates the effects of radiation, humidity and wind speed. Approximately 0.8 of pan evaporation gives an estimate of potential transpiration. Thus, using historical records of pan evaporation from a site should give a likely frequency of future sterility at that site, especially if the pan evaporation can be calibrated for one season against measured sterility. The appropriate pan data would be from the phase around flag leaf ligule emergence. Sterility would be increased beyond the estimate in instances where drought and waterlogging had closed the stomata. Clearly, there will also be variation in these estimates between sites if different genotypes have been used.

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Genetic Variability and Possible Genetic Advance for Sterility Tolerance in Wheat (*Triticum aestivum* L.) through Breeding

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Abstract

Sterility in wheat is becoming one of the most important constraints to wheat production in Nepal. Cold temperatures during the reproductive phase at higher elevations and low concentrations of available soil boron at lower altitudes are the two major causes identified. Research in the last three decades has been concentrated on husbandry practices to tackle the problem, but there have been few practical recommendations made for the farmers. Earlier studies had indicated genetic variation for relative tolerance to both types of sterility. However, all types of soils, irrespective of altitude and cropping patterns, are deficient in available soil boron. Consequently, it is very likely that low-boron-induced sterility has been confounded with cold-induced sterility.

In this study , well adapted modern varieties such as L-52, NL-297, Annapurna-3 and Paudur Local (a landrace) were identified as sterility-tolerant parents and included in a crossing program. Broad sense heritability (h^2) and genetic gains for sterility tolerance were measured. Broad sense heritability of the means of the F_2 and F_3 plants for sterility tolerance was between 14% and 53%. Progeny of Annapurna-3/RR-21, Annapurna-3/BL-1142, Paudur Local/BL-1022 and Paudur Local/NL-297 showed transgressive segregation for sterility tolerance. The predicted genetic gain for sterility tolerance by early generation selection was between 10% and 44%. High predicted genetic gains from selection at early stages in some families were found, but further studies need to be conducted to prepare for a program to develop sterility-tolerant varieties.

WHEAT (*Triticum aestivum* L.) is the third most important food crop in Nepal after rice and maize. It is the most important cereal crop during winter. There are two wheat production belts in Nepal. The first is by far the best and largest, containing the *terai*, *tar* and low hills (up to 600 m). The second belt includes the warm temperate to cool temperate mid to high hills (600 to 2000 m) (Sthapit 1995). Distinct cropping systems have evolved in these regions. Wheat is grown in both rice-based and maize-based cropping systems, but more than 80% of wheat cultivation is in the rice–wheat system (Hobbs 1990). The area planted to wheat in this system is currently 634 000 ha. This makes a significant contribution to the total food production of the country. In spite of a significant increase in the area under wheat in recent years, the productivity of the crop is still low, at 1.44 t/ha (MOF 1995).

Climate in the hilly areas ranges from subtropical to warm and cool temperate. Rainfall varies from 800mm to > 5000 mm and annual temperatures range from 5° to 25°C. Land types, soil types and irrigation systems vary (Sthapit 1995). There is great variation in the nutrient status of soils (Vaidya et al. 1995). A recent analysis of soil fertility in the mountains of Nepal revealed that all soils from 240 m to > 1600 m are deficient in available boron, irrespective of land use (Table 1). A concentration of < 1 ppm is considered deficient (Landon 1992). On average, bari land (unbunded, unirrigated uplands) has slightly more boron (0.65 ± 0.03) than khet land (bunded, irrigated terraces) (0.51 ± 0.03 ppm). Soil boron concentration is directly associated with altitude in bari lands, but the opposite is true of khet lands. Part of the explanation might be that bari lands receive more organic manures in the higher hills than khet lands, whereas khet lands are more intensively cultivated in the lower hills. Nevertheless, boron is deficient in both cases.

Boron is one of the seven essential micronutrients required for the normal growth of most plants, and has a marked effect when either deficient or in excess. Boron is readily leached. It is estimated that there is a 30% reduction in soil boron concentrations after a 25 mm rainfall. The occurrence of such a fall during the reproductive stages is also likely to cause boron deficiency

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(Ralph 1992). On some soils there is a strong likelihood of overdose if boron is applied in consecutive years. There is a narrow range between soil boron concentrations causing deficiency symptoms and those causing toxicity symptoms in plants. This narrow range presents a particular problem when dealing with poorly literate farmers and in areas where the agricultural extension system is weak. In these areas, breeding may be the best long-term option to overcome boron problems (Keren and Bingham 1985; Graham et al. 1991).

A recent adoption study conducted by Lumle Agricultural Research Centre (LARC) revealed that the mean adoption rate of improved wheat genotypes was only 49% (LARC 1995). Reasons given for not trying improved varieties or for dropping them from cultivation included sterility sensitivity as a perceived important problem. According to Sthapit and Subedi (1990a), the major threat to future wheat production in Nepal, assuming no drastic disease virulence or socioeconomic change, is a steadily increasing sterility problem. Research during the last 10 years at LARC has shown that sterility is associated with low concentrations of available soil boron in the low hills and river valleys (< 1100 m), and with low temperatures during the preanthesis to anthesis period in the mid to higher hills (> 1100 m) (Sthapit et al. 1989; Subedi and Budhathoki 1994). These causes might interact with each other, thereby making the situation more complex. Indeed, as available soil boron is deficient across all ranges of altitude, it is highly likely that sterility induced by boron deficiency can be confounded with cold-induced sterility.

Surveys done by LARC have indicated that varieties differ in their degree of cold-induced sterility and that this variation occurs in both the maize–wheat and rice–wheat production systems (Sthapit and Subedi 1990a, b; Subedi et al. 1993). There has been no systematic study to confirm this, however, and most of the surveys done on commercial varieties or breeding lines have revealed variable results. Other studies have also shown that there is great variation between wheat genotypes in sensitivity to boron deficiency as well as in response to applied boron (Mandal and Das 1988; Rerkasem et al. 1989).

Studies carried out in Nepal and elsewhere have been focused on alleviating the problem through manipulation of crop husbandry. No wheat varieties have consciously been bred in Nepal for either low temperature tolerance or boron deficiency tolerance. Even the recent strategy of the National Wheat Research Programme (NWRP) does not include breeding for sterility tolerance as an objective. Furthermore, only a meagre effort has been made to examine the possibility of using local landraces of wheat in breeding programs to develop sterility-tolerant varieties. These technologies are easily transferable to illiterate farmers without serious hazard.

The purpose of this paper is to explore the possibility of developing sterility-tolerant wheat lines as a practical means of managing the problem.

Materials and Methods

Genetic material

LARC initiated a small crossing program in wheat during 1992. One of the objectives was to produce varieties of wheat for both rice–wheat and maize–wheat ecosystems that would have sterility tolerance. Some landraces adapted to the local environment (characterised by frequent chilling), such as Paudur Local, and locally adapted modern varieties, such as Lerma-52, NL-297 and Annapurna-3, were identified as sterility-tolerant genotypes and were included in the crossing

Table 1. Status of available soil boron in the Research Command Area of LARC (unpublished data). Numbers in parentheses are sample sizes

Agroecological zone	Altitude (m)	Khet	Bari
High hills	> 1601	0.44 ± 0.07 (9)	0.70 ± 0.05 (40)
Mid hills	1001–1600	0.45 ± 0.07 (31)	0.79 ± 0.07 (54)
Low hills	601–1000	0.53 ± 0.06 (39)	0.50 ± 0.05 (39)
Besi	240–600	0.62 ± 0.07 (22)	0.46 ± 0.06 (18)
All zones		0.51 ± 0.03 (101)	0.65 ± 0.03 (151)

program. The F_2 and F_3 populations derived were grown in the 1994–95 winter at LARC's Khumal *bari* (1675 m), where chilling is frequent, in a maize/millet – wheat system under a rainfed, partially irrigated treatment. Bulk planting arrangements were used and seeds were widely spaced. Evaluations were made under natural conditions where control varieties showed high spikelet sterility. The environment during the growth period was favourable to the development of sterility. Temperatures fell to below 5°C and occasional frosts occurred. Evaluations were made under natural conditions where parental checks showed high spikelet sterility.

F_2 generations were derived from three crosses: Annapurna-3/RR-21, Annapurna-3/BL-1142 and BL-1135/Paudur Local. F_3 generations were derived from four crosses: Paudur Local/NL297, Paudur Local/BL-1022, Annapurna-3/NL-297 and L-52/NL-297. The sterility-tolerant parents were Annapurna-3, Paudur Local and NL-297.

Analysis

Different numbers of spikes were sampled from different segregating lines to represent the size of the population. To estimate sterility percentage, the number of florets per spike and the number of grains per spike were estimated and used in the following formula (Sthapit 1988):

$$\text{spikelet sterility (\%)} = \frac{\text{florets / spike} - \text{grains / spike}}{\text{florets / spike}} \times 100$$

Mean and variance of individual F_2 and F_3 plants and parents were determined. A method proposed by Mahmud and Kramer (1951) to estimate broad sense heritability on a single plant basis was used. The method involves the measurement of a trait on F_2 plants of a single-cross population and on the inbred parents used to form the population. The formula used was:

$$h^2 = \frac{\sigma^2 F_2 - \sqrt{(\sigma^2 P_1)(\sigma^2 P_2)}}{\sigma^2 F_2}$$

where:

h^2 = heritability

$\sigma^2 F_2$ = phenotypic variance among F_2 plants and includes the additive, dominance and epistatic genetic variance

$\sigma^2 P_1$ and $\sigma^2 P_2$ = phenotypic variance among parent plants.

The predicted response to direct selection (R) was estimated as $R = h^2 S$, where h^2 is the heritability of the selected trait and S is the unstandardised selection differential, calculated as the difference between the mean of selected families at 10% selection intensity and the overall population mean (Falconer 1989). Where the h^2 estimate was not available, another source was used to give indicative genetic gain (Jamjod et al. 1992).

F_2 and F_3 lines of wheat were studied for variation in sterility tolerance. The frequency distributions for percentage sterility of individual plants were grouped into ten equal classes from zero to 100. The percentage sterility of parental lines has been used as given by Subedi et al. (1993) and Subedi (1993). A t-test was done between the parental lines and 10% selected individuals and between the 10% selected individuals and the unselected population to determine the statistical difference between mean values. The predicted genetic gain of various traits was also estimated as a percentage of the original unselected population mean of F_2 and F_3 generation lines of wheat.

Results

Genetic variation of F2 generation lines

Three F_2 crosses were studied for their variation in percentage sterility. Significant differences were found between lines. The progeny of BL-1135/Paudur Local had a degree of segregation. The mean percentage sterility was 39.5% for BL-1135 (the sensitive parent) and 9.9% for Paudur Local (the tolerant parent) (Table 2). Frequency distribution for spikelet sterility in F_2 families of selected lines was determined (Fig. 1a–c). The mean percentage sterility for the population of this cross ranged from 19.0% to 42.6%.

The progeny of Annapurna-3/RR-21 were evaluated for tolerance to sterility. They were found to be significantly superior to RR-21 ($P < 0.05$) but not to Annapurna-3 ($P < 0.05$) (Table 2). The progeny of BL-1135/Paudur Local performed similarly. Percentage spikelet sterility in selected individuals of this cross was significantly less than in BL-1135 ($P < 0.001$) but not statistically different from that in Paudur Local ($P < 0.05$). Progeny of Annapurna-3/BL-1142 were significantly superior to both the parents ($P < 0.05$).

The variability in sterility was found to be

Table 2. Comparative percentage sterility and selection differential (S) for F_2 generation lines of wheat for sterility at 10% selection intensity

Cross	Parentage	Sample size	Mean percentage sterility				σ	S^d	h^2	R^e	Gain $\%^f$
			$P_1{}^a$	$P_2{}^a$	F_2 popn^b	F_2 selected individual^c					
LW-93005	BL-1135 / Paudur Local	100	39.5	9.9	42.6	7.0	27.9	35.6	0.53	18.8	44.1
LW-93002	Annapurna-3 / RR-21	20	23.0	38.7	24.9	7.1	13.2	7.8	0.14	2.5	10
LW-93003	Annapurna-3 / BL-1142	20	23.0	30.5	19.0	2.8	11.6	16.2	0.48	7.8	33.8

a: values adapted from Subedi et al. 1993
b: mean spikelet sterility of unselected F_2 population
c: mean of selected population at 10% selection intensity
d: calculated as difference between b and c
e: $R = h^2 \times S$
f: gain % = (R ÷ mean of unselected population) × 100

quantitative and could be associated with the segregation of multiple minor genes or polygenes that are influenced by environment. The common feature of all these crosses was that the progeny are mostly clustered around the mean of the better parent (Fig. 1a–c). Although the mean percentage sterility of Paudur Local was quite low (Table 2), this variety lacks other desirable traits to be widely acceptable. However, the variation created through combinations with BL-1135 has provided useful material for making a genetic advance over BL-1135 for sterility tolerance (Fig. 1a).

Analysis of the percentage sterility of a segregating population and of selected individuals also suggests hope for breeding sterility tolerance. Statistical evaluation between the unselected population and the 10% selected individuals of all three crosses also revealed significant differences between them ($P < 0.05$). These findings indicate a transgressive segregation for two crosses, Annapurna-3/RR-21 and Annapurna-3/BL-1142. The mean percentage sterility of selected individuals is significantly superior to that of both parents. The selection of sterility-tolerant segregants superior to the better parent is possible, as shown in Figure 1. It is apparent from Table 2 that the mean percentage sterility of selected individuals from different crosses was quite low. The broad sense heritability (h^2) of the means of the F_2 plants for sterility tolerance was medium in the BL-1135/Paudur Local cross and in the Annapurna-3/BL-1142 cross but was low in the Annapurna-3/RR-21 cross (Table 2). Experiments done in other countries found that broad sense and narrow sense heritabilities for boron deficiency tolerance in wheat were 0.50–0.58 and 0.35–0.42 respectively (Jamjod et al. 1992).

The predicted genetic gain for sterility tolerance by early generation selection for reduced spikelet sterility among F_2 families in BL-1135/Paudur Local was 44.1% at 10% selection intensity (Table 2). This is considered promising. The estimate of h^2 was not accurate, as the variance of F_2 was attributed to genotype by environment interaction and error variation, but the mean percentage sterility of the 10% selected individuals was so low that genetic gain by selection is possible.

Genetic variation of F_3 generation lines

The results for F_3 generation lines are similar to those for F_2 lines. The progeny of Paudur Local and NL-297 showed great variation in percentage sterility, even though the sterility of both the parents was less than 15% (Table 3). Statistical analysis of the difference between parents and 10% selected individual progeny of Paudur Local/NL-297 showed that sterility tolerance of the 10% selected individuals was significantly superior to that of both parents ($P < 0.01$). Although the possibility for genetic gain for sterility tolerance over Paudur Local was not much, there is a strong possibility of making genetic gain over NL-297 as there is a significant difference between the selected population and NL-297 ($P < 0.01$). This might be possible because of transgressive segregation.

Progeny of Paudur Local/BL-1022 showed a significant difference between the 10% selected individuals and their parents ($P < 0.01$). It is also evident that most of the population has an advantage over both parents (Fig. 2b). There was no difference, however, between the progeny of Annapurna-3/NL-297 and L-52/NL-297 ($P < 0.05$) (Table 3). The F_3 generation progeny of Paudur Local/BL-1022 and Paudur Local/NL-297 showed a general trend of transgressive segregation, as the mean percentage sterility of all the progeny was significantly less than the mean of either parent ($P < 0.01$).

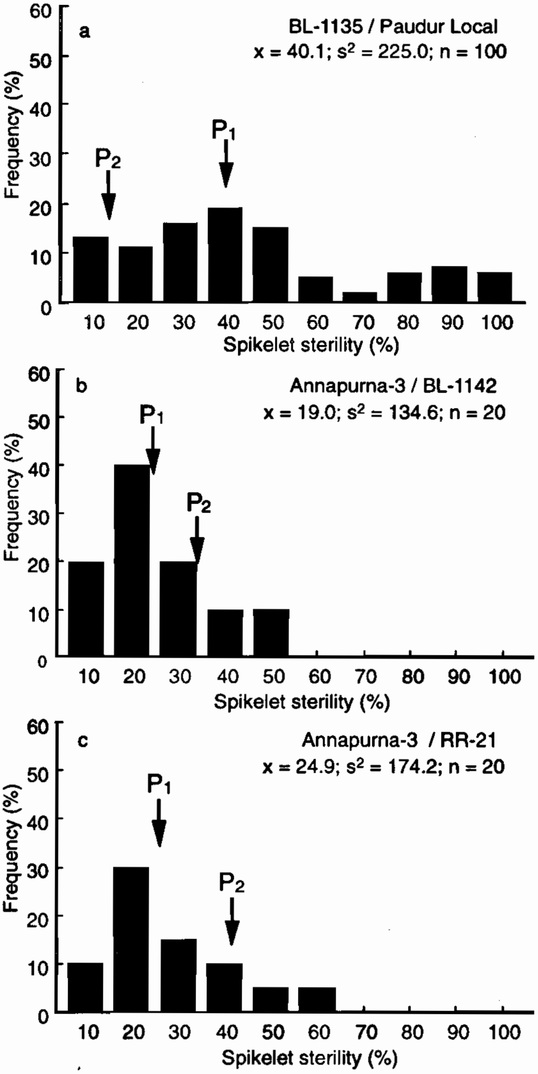

Figure 1. Frequency distribution of spikelet sterility (%) in F_2 families of four wheat crosses under chilling stressed conditions in Nepal, 1994–95

Progeny of Paudur Local/BL-1022 have also produced a useful result. About 10% of the progeny of this cross have shown genetic superiority to the tolerant parent (Table 3). That population should provide a suitable base for developing sterility-tolerant varieties from a BL1022 background, which will be important not only for the hills but for the terai as well.

In absence of h^2 estimates for F_3 families, information from Jamjod et al. (1992) was used to predict indicative genetic gain by selection. The high variance and possible moderate h^2 estimates between F_3 families resulted in high predicted genetic gains from selection. Using $h^2 = 0.42$ as the narrow sense heritability (as reported by Jamjod et al. (1992)), the predicted indicative

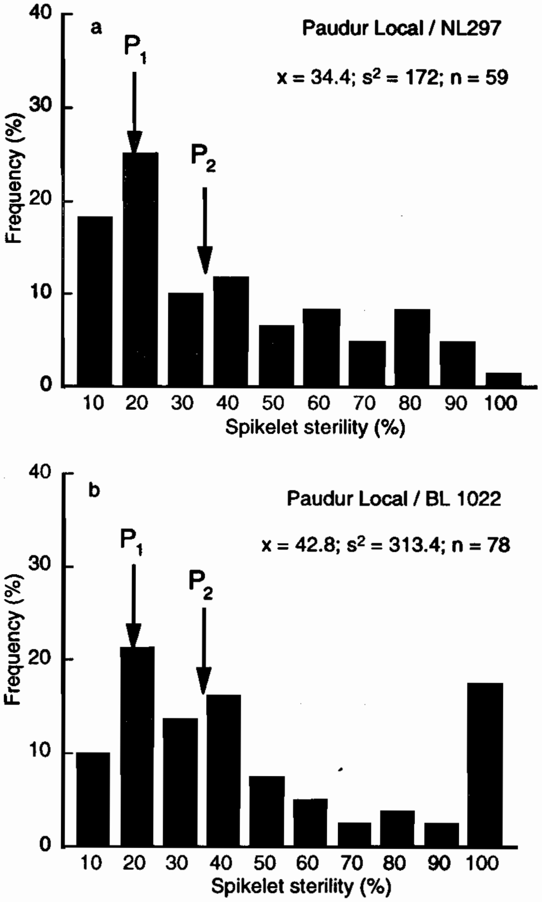

Figure 2. Frequency distribution of spikelet sterility (%) in F_3 families of four wheat crosses under chilling stressed conditions in Nepal, 1994–95

Table 3. Comparative percentage sterility and selection differential (S) for F_3 generation lines of wheat for sterility at 10% selection intensity

Cross	Parentage	Sample size	Mean percentage sterility				σ	S^d	$h^{2\,(e)}$	R^f	Gain %^{g}
			P_1^a	P_2^a	F_3 popn^b	F_3 selected individual^c					
LW-92001	Paudur Local/ NL-297	59	13.8	15.0	34.4	3.4	25.7	31.0	0.42	13.0	37.8
LW-92014	Paudur Local/ BL-1022	78	13.8	31.3	42.9	4.9	31.6	38.0	0.42	15.9	37.2
LW-92021	Annapurna-3/ NL-297	20	20.1	15.0	25.8	5.3	13.5	20.5	0.42	8.6	33.3
LW-92022	L-52/ NL-297	20	18.6	15.0	28.8	4.1	13.3	24.7	0.42	10.4	36.0

a: values adapted from Subedi et al. 1993 b: mean spikelet sterility of unselected F_2 population c: mean of selected population at 10% selection intensity d: calculated as difference between b and c e: value adapted from Jamjod et al. (1992) f: $R = h^2 \times S$ g: gain % = (R ÷ mean of unselected population) × 100

genetic gain for F_3 families ranged from 33.3% to 37.8% (Table 3). Using the broad sense heritability figure of 0.53 based on results of the F_2 generation, the predicted gain was between 42.1% and 47.8%. In the F_3, in both crosses where Paudur Local was used as a parent, the improvement in percentage sterility over both parents was statistically significant. The percentage of genetic gain was also higher in those progeny. The results of the study indicate that selection for cold-induced sterility-tolerance by direct selection is effective. Work of Jamjod et al. (1992) also supports the idea that similar progress can be made for wheat sterility induced by boron deficiency.

Discussion

The present study of F_2 and F_3 lines of wheat for a segregating pattern of sterility has shown a clear trend of improvement in tolerance to sterility over the better parents.

It could be argued that the variation in the segregating population was caused by the environment. However, LARC's coordinated varietal trial in 1994–95 (Subedi et al. 1995) also revealed that sterility ranged from 13% to 94% among wheat genotypes. The landrace Paudur Local was found to be tolerant to cold-induced sterility and can also be a valuable donor for breeding tolerant wheat varieties. All these findings augur well for the future in reducing sterility by breeding.

Many researchers have suggested that adjusting planting dates could reduce the effects of cold-induced sterility. Several studies done at LARC have shown that early maturing varieties sown early are most susceptible (Sthapit et al. 1989; Subedi and Budhathoki 1994). On the other hand, yield declines linearly for plantings after the third week of November. Indeed, it is not possible to grow a profitable, late-sown wheat crop under rainfed conditions (Sthapit 1995). Decline in yield in late-sown crops could be due to moisture or heat stress, an increased likelihood of rust, and lower efficiency of use of applied nitrogen (Hobbs 1990). Therefore late planting of wheat in the mid to high hills might not be a suitable proposition considering the tight cropping patterns adopted and the high yield penalties (Joshi et al. 1994).

Sterility associated with boron deficiency is becoming increasingly important in warmer areas. Most workers agree that the magnitude of the problem is very high, that wheat genotypes differ in their sensitivity to soil B, and that genetic variability for sensitivity to B should be properly used in breeding and selection. It now appears that significant genotypic variation for tolerance to boron deficiency exists in segregating lines. The trait is under additive gene action, with 50% to 58% broad sense and 35% to 42% narrow sense heritability. Consequently, direct selection for tolerance to boron deficiency should be effective (Jamjod et al. 1992). Varieties with built-in tolerance to salt, nutrient and metal toxicities and nutrient deficiencies will enable small-scale farmers to obtain reasonably stable yields by using management inputs they can afford (Singh 1991). This will be more important in Nepal, where available soil boron is deficient across all ranges of altitude.

For the farmer the genetic improvement of crops offers the most cost-effective means of increasing or maintaining profitability (PBI 1990). A recent study in Nepal on returns to wheat research has shown that benefits realised during the Green Revolution resulted mainly from the adoption of improved germplasm. Now, benefits of wheat breeding research will be achieved mainly through regular varietal replacement (Morris et al. 1992) plus the adoption of modern varieties in more remote areas with limited access to extension services.

An advantage of tolerant genotypes is that they continue to yield well until stress becomes severe (Joshi 1976; Sharma 1987). Such varieties also put no additional financial burdens on farmers. There is also the view that the genetic approach is more relevant to developing countries as they often face severe constraints to the availability of inputs (Singh 1991). It must not be overlooked while setting research priorities, however, that illiterate farmers could lose crops to sterility induced by B toxicity because of overfertilising.

The double haploid breeding system in wheat × maize crosses has been reported to be successful in developing salt-tolerant wheat varieties (Laurie et al. 1990; Witcombe 1995). Chromosome elimination in early embryo development leads to production of haploid wheat embryos in such crosses. This technique can be usefully employed in breeding wheat lines tolerant to boron deficiency.

Future Areas of Research

Although ample information exists on the inheritance and gene action of both deficiency and toxicity of boron in wheat, such information is lacking for local landraces and agronomically accepted varieties of wheat in Nepal. Therefore the following activities need to be conducted:

- Collection of local landraces of wheat from the far western hills of Nepal and screening them for sterility induced by cold and boron deficiency.
- Identification of suitable parents for tolerance to cold and boron deficiency for inclusion in a crossing program.
- Study of heritability of tolerance to cold and boron deficiency in wheat.
- Use of the double haploid breeding system for breeding sterility-tolerant wheat varieties.

Wheat planting in Nepal is dictated by rice varieties, which are mostly of medium to late maturity. Therefore, efforts should be made to breed early maturing rice varieties with acceptable grain quality and high yield potential. There is a need for integrated approaches to deal with different issues of the rice–wheat system.

Conclusion

Sterility is becoming one of the most important production constraints to wheat in Nepal. Cold temperature during preanthesis and anthesis and low concentrations of available soil boron have been identified as the two major factors responsible for this problem. Almost three decades of work on the topic has been focused mainly on crop husbandry practices to alleviate the problem. However, considering the inherent boron deficiency of Nepalese soils, its interaction with varieties and temperatures, and several technical problems associated with the safe use of boron when dealing with poorly literate farmers, it is unlikely that practical remedies can be found through husbandry practices. The current preliminary study of genetic variability for sterility tolerance in wheat lines has shown good promise. High predicted genetic gains from selection at F_2 and F_3 stages indicate that there is a chance that this problem can be overcome by breeding. A number of systematic studies need to be conducted before launching a specific breeding program for sterility tolerance in wheat.

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Summary

Overview: Trends and Implications

H. M. Rawson*

Aims of the Project

The aims of the project are outlined in the Foreword to these Proceedings. In brief, they were to document our understanding of what causes sterility in wheat in the subtropics of Asia and air our perceptions; to carry out experiments that might test these notions in controlled environments or in field studies in all collaborating countries; and to collate these studies and reassess our understanding of the problem to try to provide some solutions.

State of Understanding

In subtropical Asia, wheat production has increased from negligible amounts in the late 1960s to an annual production of 1 to 1.5 million tonnes in Bangladesh (Saifuzzaman and Meisner, these Proceedings), nearly 1 million t in Nepal (Devkota, these Proceedings), and more than 7 million t in Pakistan (Siddiqui, these Proceedings). Sterility had been variously estimated to cause total crop loss in some locations in the worst years yet negligible effects in other years (see the general survey by Rerkasem and individual country papers in these Proceedings, namely, Rerkasem et al., Saifuzzaman, Subedi et al. ('Sowing Time') and Yang et al.).

Although boron deficiency has been unquestionably associated with much of the sterility, particularly in Thailand and Dehong Prefecture, China, considerable variability between locations and years had led researchers to conclude that other factors, possibly environmental, modified the response to boron. It was also suspected that factors such as low temperature at key plant developmental stages might cause sterility independently of boron limitation in Nepal and Bangladesh. Water stress was considered to be the only serious problem in Pakistan. Genotypes have been developed or identified that have varying degrees of ability to minimise sterility, but none is available that is fully fertile in all conditions.

Common Field and Controlled Environment Research

This ACIAR project provided a unique opportunity to bring experts from the region into a shared field experiment spanning five countries (six sites) in the Asian subtropics. The field experiment was designed assuming that much of the problem of sterility was associated with boron deficiency. As such, it had two common genotypes of wheat at all sites, Fang 60 and SW 41, which had been shown many times in Thailand to be relatively tolerant (Fang 60) and susceptible (SW 41) to low soil boron (e.g. Rerkasem 1993). At each site, local genotypes were added for comparison. The experiment had two rates of boron: either none or 1 kg/ha was added to the soil. The six locations were Dehong Prefecture, China; Chiang Mai and Samoeng, Thailand; Tandojam, Pakistan; Rishing Patan, Nepal; and Dinajpur, Bangladesh. These locations and the three planting dates at each provided the 18 environments to which the two common genotypes were subjected. Sterility as described in Rerkasem's 'Survey' paper (these Proceedings) had previously been observed at all locations, apart from Tandojam, which was the control location. Plant samples from each site were assessed for flag leaf and ear boron concentration at the one centre (Chiang Mai) to avoid any analytical errors between research groups owing to discrepancies in methods.

Research was also done in controlled environments. It also centred on boron as the prime cause of sterility. The research at Murdoch University focused on interactions between low temperature and boron (Huang et al., these Proceedings). That done at CSIRO Canberra considered boron,

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temperature, radiation, humidity and genotype as factors (Rawson et al., Rawson and Noppakoonwong, these Proceedings).

Expectations

All researchers naturally expected that their preconceived notions about the causes of sterility in their areas would be upheld (see Foreword), and to a degree this is reflected in papers in these Proceedings. It was also expected that, as sterility can be quite elusive, there could be several environmental combinations that would not lead to problems. Being able to define those positive and negative combinations of conditions was the aim, so that recommendations could be made on how to avoid the deleterious combinations or how and when to apply ameliorative treatments.

Findings of the Field Studies

Did the 18 environments differ?

In terms of temperature, the environments differed considerably. Mean temperatures ranged from 12° (Dehong) to 26°C (Chiang Mai) at sowing, and from 17° (Nepal) to 24°C (Chiang Mai) at anthesis (Table 1). The daily maximum and minimum temperatures varied much more. The initial workshop had identified the stage from flag leaf ligule emergence (FLE) to anthesis as probably covering the period when wheat plants are particularly sensitive to the environment and when deleterious conditions will lead to sterility. Mean temperatures during that stage ranged from 14° to 25°C, but that temperature range included minimum values below 6° and maxima above 34°C. The cooler sites were Dehong, Nepal and Pakistan.

Temperature changed phenological development

The crops took different times to reach anthesis from the various plantings. In Dehong, for example, even though the plantings spanned a full month, anthesis occurred over only eight days. In Chiang Mai, where mean temperatures changed relatively little throughout the season, there was no such convergence with advancing development. The different patterns of phenological development at different locations and planting dates were due very largely to differences in temperature.

Table 1. Temperatures at sowing, flag leaf ligule emergence (FLE) and anthesis from the studies in Rishing Patan (Nepal), Chiang Mai (Thailand) and Tandojam (Pakistan), and the numbers of days and degree days (DD) to these stages assuming a base temperature of 0°C throughout (first bold column) or a base temperature of 0°C from sowing to FLE and a base temperature of 7°C from FLE to anthesis (second bold column)

Date sown	°C at sowing			Sowing to FLE		°C at FLE			Sowing to anthesis*		°C at anthesis			FLE to anthesis		Sowing to anthesis†
	min.	max.	av.	days	DD > 0°	min.	max.	av.	days	DD > 0°	min.	max.	av.	days	DD > 7°	DD
Nepal																
21 Nov	12	25	19	67	1056	8	20	14	90	**1435**	10	23	17	23	220	**1276**
6 Dec	11	24	17	67	1025	10	23	17	88	**1390**	12	26	19	21	221	**1246**
21 Dec	8	23	16	67	1031	10	23	17	82	**1347**	13	28	21	15	179	**1210**
Thailand																
18 Nov	19	33	26	47	1081	13	29	21	59	**1336**	15	30	23	12	171	**1252**
13 Dec	14	31	22	47	1040	17	33	25	53	**1200**	15	30	23	6	118	**1158**
28 Dec	15	29	22	45	1001	14	31	23	54	**1213**	14	33	24	9	149	**1150**
Pakistan																
13 Nov	15	35	25	60	1125	6	25	16	79	**1525**	10	28	19	19	129	**1254**
30 Nov	13	34	24	63	1154	12	28	20	80	**1446**	8	29	19	17	211	**1365**
17 Dec	9	29	19	61	1172	8	29	19	76	**1346**	9	28	19	15	171	**1343**

Thus, although crops took between 53 days (Chiang Mai) and 90 days (Nepal) to reach anthesis, if this time is expressed as accumulated thermal time (i.e., the sum of daily mean temperature for each day between sowing and anthesis), the differences become quite small. Table 1 shows the calculation of thermal time assuming a base temperature of 0°C (see Rawson 1993 for an explanation of this). It also shows a more realistic summation using a base of 0°C to FLE followed by a base of 7°C from then to anthesis (Slafer and Rawson 1995). The calculations are for the average performance of Fang 60 and SW 41.

The observation that variation in the timing of events is determined primarily by temperature means that we can predict fairly accurately when critical developmental stages such as FLE are likely to occur if we know what the mean temperatures are likely to be. Calculation of the simple accumulation of mean temperature converted a difference of 22 days between locations for the timing of FLE (45 at Chiang Mai to 67 in Nepal) to a difference of only 55 degree days. This is equivalent to a difference of only 2.5 days at the mean temperature of Chiang Mai. In the worst case, and using this crude calculation, we could estimate to within one week when Fang 60 or SW 41 would reach FLE anywhere in this region. Sophisticated models would do better.

Yield and the small effect of added boron

Yield across the region was variable but generally good. For Fang 60, which is unresponsive to boron deficiency, it was surprisingly good (Table 2), considering that Fang 60 is an old variety (released in Faisalabad in 1977) and that it was not bred for all these countries. 'Late' planting resulted in poorer yields at all sites, usually because of water stress and increasing temperature shortening the grain filling phase and reducing kernel weight (see individual papers).

Table 2. Yield of Fang 60 (t/ha) at each location and sowing date

	Sowing date		
	I	II	III
Bangladesh	4.8	5.2	4.0
Nepal	4.2	3.6	2.7
Dehong	2.5	2.3	1.8
Chiang Mai	2.1	2.4	1.3
Samoeng	2.1	2.1	1.7
Pakistan	5.8	5.7	4.1

Surprisingly, there were no significant grain yield responses to boron application at field sites in Nepal, Bangladesh, China and Chiang Mai (boron was not applied at Tandojam), in spite of the generally higher plant boron concentrations that followed boron fertilisation. There was a trend towards a positive response to boron at Samoeng, but no significant overall genotype by boron interaction. Thus the yield of Fang 60 did not consistently respond to boron any less, nor yield of SW 41 consistently any more, than other genotypes. Because there was no response to boron, there was no differential response to boron between planting times. This overall result contrasts with previous observations in the region.

Sterility and yield component compensation

As discussed in individual papers, sterility was assessed in two ways. The first method, developed by Drs Rerkasem and R. A. Fischer, subsamples the ear and is called the grain set index (GSI). It counts the percentage of the two basal florets with grain in the 10 central spikelets of the ear, and so assesses 20 florets in total. The second method, described as the LAC method, assesses the percentage fertility of all competent florets in the ear (see also Bagga and Rawson 1977 for use of this method). This could therefore consider anything from 20 to 80 florets, depending on the size of the ear. GSI tends to give higher estimates of fertility than LAC (13% higher overall in Subedi et al. ('Sowing Time'), these Proceedings).

Using the GSI method, there was no significant effect of any of the factors on sterility in the field trials done in Bangladesh and China. Time of planting did not change the degree of sterility at any of the six locations. Using the LAC method in Bangladesh and either method at other sites apart from Pakistan showed that there were differences between genotypes in percentage fertility. Fang 60 consistently had more grains per competent floret and SW 41 had less than the average of genotypes, in accord with expectations for these varieties. The absolute values for Bangladesh and Nepal were remarkably parallel: Fang 60 averaged 23% and 20% respectively and SW 41 averaged 30% and 29% sterility across planting dates. Nevertheless, for two such genotypes with reputed extreme differences in response to boron, a difference in fertility at these low boron sites of more than 8% might have been expected. A similar small difference between these two genotypes was observed at Chiang Mai (4%), Dehong (3%) and Tandojam (1%). Only at Samoeng did the genotypes differ considerably (28% overall), though at the first planting the difference reached only 13%. So although all trends were in the direction expected from previous years' data, the size of the difference between genotypes was generally small.

The improvement in fertility with applied boron was also smaller than might have been expected. In Bangladesh and Dehong there was no response; in Nepal, Fang 60 did not respond but SW 41 increased its fertility by 10%; and in Chiang Mai, Fang 60 and SW 41 both responded positively but minimally (6% and 4% respectively). Once again, Samoeng was the only site at which there was a marked improvement in fertility stemming from the application of boron (9% improvement in Fang 60 at the third planting and 21% overall in SW 41).

These differences in fertility between genotypes and treatments did not translate to differences in yield at most sites because the yield components tended to compensate for each other. Thus, although Fang 60 invariably had higher fertility than other genotypes, the kernels were small. Individual grains grew larger to compensate for grain misses in other genotypes.

What was different about Samoeng?

What was different about Samoeng in this year when other sites had minimal sterility, and why was there less sterility at the first planting date here? We might suspect that some adverse weather during the critical stage of FLE to ear emergence might have been implicated, particularly if it reduced the movement of boron into the plant. Before dealing with that problem it is worth paraphrasing Saifuzzaman (these Proceedings): In the 1994–95 growing season, conditions were not so adverse as in earlier years during the critical stages. Sterility was minimal in growers' fields in the sterility-prone areas. It is also worth quoting Yang et al. (these Proceedings): 'The results might not be representative of long-term trends.' The general implication seems to be that our chosen year for the study was a good year for wheat production in the area, but a poor year for sterility research.

In an attempt to assess why there was sterility at Samoeng, the date of the critical stage of FLE for SW 41 was calculated from the relationships in Table 1. Maximum temperatures, averaged across the five days around the calculated dates, were 25.2°C for the first planting date, 26.6° for the second and 28.1° for the third, and pan evaporation was 3.6, 3.1 and 4.3 mm. Not apparently very different. There was morning dew during the critical period for all treatments. However, although mean pan evaporation was similar for this stage for the three plantings, minimum daily evaporation was 1 mm at planting 2 and 2.6 mm at planting 3, lower than at planting 1. These evaporation values were all lower than during the critical stages of the field study at Chiang Mai and Dehong, where concentrations of water-soluble boron in the soil were similarly low. So it could be speculated that some critical requirement for boron, perhaps during pollen meiosis, was not being met because the poor boron supply in the soil could not be moved into the plant because the crop's transpiration rate was limited (see Saifuzzaman and Meisner, and Rawson ('Parameters'), these Proceedings, for expansion of this idea).

This speculation appears to be poorly founded, however, when attempts are made to correlate boron concentrations of the ear and flag leaves with fertility. In the Samoeng data there was no correlation. But perhaps the boron concentrations of bulk tissues have limited meaning, as suggested by Rerkasem and Lordkaew (these Proceedings), who say that it is the boron concentrations of the anthers and carpels that are correlated with sterility. Differences in boron content of these small organs, which collect their boron during only a few days, can be swamped by patterns in the bulk ear, which accumulates its boron over many days—in fact, from well before the critical phase to well after.

The critical phase and a mechanism

The critical phase for sensitivity to boron was assumed to span FLE to anthesis. The field studies were not designed to define the phase but the controlled environment transfer studies in Canberra (Rawson et al., these Proceedings) suggested that it was certainly spanned by the slightly longer period between the emergence of the second-last leaf ligule and anthesis, and was probably complete by ear emergence (Rawson and Noppakoonwong, these Proceedings). A report from Murdoch University, based on transfer studies, presented at the Lumle workshop by Bernie Dell indicated that it might begin shortly after the terminal spikelet can be identified microscopically and last for only five to ten days. Experiments in Canberra, not complete at the time of the workshop involved reciprocal transfers between B0 and B+ solutions at several dates and showed that the critical stage for boron uptake is from when the flag leaf first begins to emerge to shortly after its ligule appears (Rawson 1996). This period of one phyllochron can be as short as five days depending on temperature. If plants are unable to take up boron throughout that period, either because there is no available boron in the root medium or because transpiration is prevented, the ear associated with that flag leaf is fully sterile. If boron is unavailable for part of that period, the part of the ear at the critical developmental phase during that period is sterile. As tiller ears are not synchronous with the main ear, the tiller ear at that critical stage during the period of boron deficiency will suffer.

The studies showed that the critical stage for an ear was the same in all six genotypes examined, which included Fang 60 and SW 41. The experiments gave some inkling of a mechanism by which Fang 60 appears to be able to tolerate low boron soils. They showed that, whereas genotypes like SW 41 have no available reserve of tissue boron that can be used when external boron supply becomes unavailable, Fang 60 can mobilise a reserve of tissue boron up to three phyllochrons after it was laid down. Sonora 64 appears to be able to do this also, though to a lesser degree. So short periods of low transpiration and associated low movement of boron in the transpiration stream are of minimal consequence to genotypes like Fang 60. In them, the reserve can bridge the gap left by current uptake. It has been suggested (Rana Munns, Dale Blevins, Richard Bell, pers. comm.) that the basis of the difference between genotypes might be their composition or amount of agents that chelate the boron for transfer in the phloem (polyols such as mannitol and sorbitol).

Research in pot culture

The pot culture work in Chiang Mai, Perth and Canberra showed that when 'soil' boron is very low, sterility is very high. So even when weather conditions are not conducive to producing sterility, plants can still be sterile if soil boron is sufficiently limiting. This is particularly demonstrated in the paper by Rerkasem et al. (these Proceedings), where plants grown in low boron soil in the field were essentially fertile, whereas plants grown in sand, at the same time as the field crops and close by, were sterile. Both experiments had the same environmental conditions, but the sand had virtually no trace of boron. As proposed in many of the papers in these Proceedings, however, what is important is the balance between boron availability in the soil and the environmental conditions that mediate the movement of that boron into and through the plant to the generative zones during the critical phase (e.g. Huang et al., Saifuzzaman and Meisner, these Proceedings). It was shown that even when soil boron is in the 'adequate' range, ears can be up to 30% sterile if radiation is low and humidity and temperature are high (Rawson et al., these Proceedings). Furthermore, if plants growing in a complete nutrient solution are prevented from transpiring by enclosure in clear plastic only during the critical phase, they too are fully sterile (Rawson 1996). This could indicate that environmental conditions alone can cause sterility, but it could equally imply that the environmental conditions are reducing the plant's ability to take up the boron present in the 'soil'. Under such environmental conditions, adequate soil boron becomes inadequate. It is suggested that this change in balance happens in the field in some years and if it occurs during the critical phase of around one week, the consequences can be devastating.

Applications of the Findings and Future Directions

What are the implications of the observations? Can they be used in any way to forecast the likelihood of sterility from weather patterns and to minimise sterility in future? It helps significantly simply knowing that the critical stage begins when the flag leaf tip begins to emerge, which is earlier than previously assumed, and that factors that reduce transpiration during this phase, such as mists, long-lasting dew, low radiation, water-logging and water stress (see Devkota, Saifuzzaman and other papers, these Proceedings), are going to increase the likelihood of sterility. It is very difficult to make a link between weather conditions for a day or two at flag leaf emergence and gaping-glume sterility up to three weeks later, as our memories of anything but very extreme weather patterns are generally unreliable. But once the grower is aware of that relationship, he or she will be able to assess whether remedial treatments are economically viable; that is, what level of fertility loss is acceptable because it would be recovered naturally by yield component compensation.

The first way that the knowledge of these relationships can be used is for the grower in the sterility-prone areas to observe the weather during the critical period and avoid waterlogging the soil at that time (Saifuzzaman and Meisner, these Proceedings). If it is unusually misty, if dew is remaining on the crop beyond midday, if it is warm but heavily overcast for two to three days, or if the crop is wilting, then sterility will be a likely outcome. One approach to estimating the effect of the weather is to measure pan evaporation during the critical period, as this will give an estimate of transpiration in crops that are not water-stressed. It seemed from the multi-location field experiment described in these Proceedings that pan evaporation seldom fell below 2.5 mm a day during the critical phase, and there was minimal sterility. So above 2.5 mm may be a safe level for adequate boron uptake for all locations. Below 1.5 mm a day for a run of days might be disastrous if temperatures are warm during that period. Such measurements can generally be made only at meteorological stations. Recently, we developed a small, portable pan evaporimeter that is operated by gravity and water flow and can be made cheaply. These could be used for secondary measurements at local field sites. The design is available from CSIRO Division of Plant Industry, Canberra.

Once the grower has assessed that there is a likelihood of devastating sterility occurring, is there anything that can be done to reduce the damage? Is it too late to apply boron? As Saifuzzaman and Meisner (these Proceedings) have noted, there have been mixed responses in field studies to applications of boron by spraying. In glasshouse studies, we have found that a spray of 0.05% boric acid solution applied as late as the onset of the gaping glume stage will recover between 20% and 60% of the fertility in ears that would otherwise have been completely sterile. Earlier sprays have been more effective. In our studies we applied a very fine spray to the ears. If borax costs around $1 a kilogram, it should cost around $0.25 in chemicals to spray each hectare in such remedial treatments. It is stressed that these were glasshouse studies, but their positive outcome suggests that they should be tested further in the field, with the timing of the sprays linked to the stage of development of the crop.

One of the pluses of sterilisation by boron restriction is that it appears to affect mainly the male organs (Rerkasem and Lordkaew, these Proceedings). This means that if viable pollen is available near the male-sterile plants from occasional fertile plants, there is a likelihood of cross-pollination. Rerkasem and Lordkaew (these Proceedings) found in soils of varying but limiting boron levels that the degree of such cross-pollination could raise the grain set index by 18% to 26%, irrespective of soil boron availability (their Table 2). This was equivalent to 4 to 10 grains per ear. In an average crop with 2 million ears per hectare, this could be equivalent to a yield increase of 600 kg for 10 extra grains per ear. Of course, if the whole crop is sterilised there will be no source of fertile pollen. In areas where large-scale sterilisation is likely, and if there are alternative genotypes like Fang 60 with proven resistance to low boron that are matched to the main local genotype for date of anthesis, a planting of two mixed genotypes could be a solution.

A better solution, though a longer-term one, would be to breed new lines with the low boron tolerance of Fang 60 and the duration, yield and quality characteristics required for the region. Joshi and Sthapit (these Proceedings) discuss with optimism the likely outcomes of a breeding program designed to minimise low boron and low temperature sterility. With any breeding program, progress is accelerated if there is a defined screening procedure for progeny. Breeding for tolerance to low boron in field plots is very difficult because of the effect of the weather on low-boron-based fertility, the unpredictability of the weather, and the short duration of the critical phase. For example, in breeding plots where there was a difference in anthesis dates of a few days between genotypes, a short period of misty weather could sterilise one genotype but not another, solely because one genotype was at the critical phase and the other was not. The incorrect conclusion could be that there was a difference in sterility tolerance between genotypes. This supposed tolerance would be unlikely to appear in subsequent selections. A possible screening procedure for low-boron tolerance could use the pot and gravel culture method (Rawson 1996) and transfers of plants from adequate to zero boron during the critical stage. If a prime difference between low-boron-sensitive and tolerant plants is a capacity to maintain an accessible reserve of tissue boron as discussed above, this procedure would work.

Several of the papers presented at the meeting drew attention to the problem of low temperature tolerance causing sterility, and noted that genotypes differ in their tolerance. However, none indicated exactly when and for how long in development the crop might be sensitive, though there was a general belief that the sensitive stage is around anthesis. None gave data on the critical screen or tissue temperature for damage. No one could say whether that critical temperature changes with development, and to what degree the low temperature response interacts with a low boron response. All we can conclude from the studies presented is that a minimum screen temperature of 5°C causes no damage (Huang et al., these Proceedings) but that temperatures below 5°C can (see Tiwari, these Proceedings). Tiwari also noted from a brief experiment that the duration of cold (1 to 24 hours at anthesis) did not alter the degree of sterility. Although this ACIAR small project has provided insight into how soil boron limitation might be associated with sterility and how the effects depend on the weather, it is still necessary to answer questions relating to low temperature and its interaction with boron before we can say that we understand what causes sterility in wheat.

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