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**Effects of Pre-anthesis Drought Stress and Nitrogen on
Yield, Nitrogen Use Efficiency, and Grain Minerals of
Tropical Maize Varieties**

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ABBREVIATIONS

(Definitions see chapter in brackets)

AFNR	Apparent recovery of mineral fertilizer nitrogen (3.6.4.)
ANM	Apparent nitrogen mineralization (3.2.)
ASI	Anthesis-silking interval (3.6.2.)
CIMMYT	Centro Internacional de Mejoramiento de Maíz y Trigo
DaE	Days after emergence
DM	Dry matter
DS	Drought-stressed
E_{pan}	Pan evaporation (3.5.3.)
ET_{crop}	Evapotranspiration crop (3.5.2.)
FM	Fresh matter
GDD	Growing degree days (3.5.1.)
HI	Harvest index (3.6.3.)
K_c	Crop coefficient (3.5.2.)
K_p	Pan coefficient (3.5.3.)
LAI	Leaf area index (2.4.1.)
LRI	Leaf rolling index (3.6.1.)
NHI	Nitrogen harvest index (3.6.4.)
N_{min}	Soil mineral nitrogen (NO_3 -N) (3.2.)
NUE	Nitrogen use efficiency (3.6.4.)
NUtE	Nitrogen utilization efficiency (3.6.4.)
OPV	Open-pollinated variety
SNC	Shoot nitrogen concentration (3.6.4.)
TKW	1000-kernel weight (3.6.3.)
TSN	Total amount of shoot nitrogen
V_x	Plant development / leaf stage (3.4.)
WUE	Water use efficiency (2.2.)
WW	Well-watered

1. SUMMARY

In the tropics, water and nitrogen (N) are the factors that limit the grain yield of maize (*Zea mays* L.) the most. The risk of water shortage in Thailand is greatest during the vegetative stages of maize development. A three-year study with two water regimes (pre-anthesis drought vs. irrigation throughout the vegetative phase), three levels of N fertilization (0, 80, 160 kg N ha⁻¹), two open-pollinated varieties (Suwan 1 and La Posta Sequia), and two hybrids (KTX2602 and DK888) was conducted in the tropical lowlands of Thailand on an ustic, isohyperthermic, kaolinitic oxisol. The main aim of the study was to determine the interactive effects of pre-anthesis drought stress, N fertilizer rate, and variety on the grain yield, yield components, and harvest index of maize. Several N-related parameters, such as the total amount of shoot N, N utilization efficiency (grain yield per unit shoot N), shoot N concentration, N harvest index (proportion of grain N to total amount of shoot N), and apparent fertilizer N recovery, were investigated to determine their suitability as breeding traits for increased N use efficiency. A further objective was to determine whether the grains of tropical maize varieties have different concentrations of minerals and to which extent varietal differences are affected by the availability of N and water.

Averaged across the N rates and varieties, drought-stressed maize yielded 32% (1995), 13% (1996), and 21% (1997) less than well-watered maize. Irrespective of the variety, 80 kg N ha⁻¹ were sufficient to achieve maximum grain yield under pre-anthesis drought, whereas more than 160 kg N ha⁻¹ seemed to be required for maximum yield in the well-watered environment. Pre-anthesis drought significantly reduced the number of kernel rows, the number of kernels per row, as well as the 1000-kernel weight; the effect of the water regime on the ear number of the semi-prolific DK888 varied from year to year. Drought stress consistently resulted in marked increases in the harvest index. There were significant effects of the water regime by variety interaction on grain yield in two of the three cropping seasons (1996 and 1997). KTX2602 was more affected by drought than Suwan 1 in all the years and, in two of the three years more than La Posta Sequia. This was attributed to the fact that KTX2602 was the earliest variety. In 1997, the strong grain yield response of DK888 to continuous irrigation was probably responsible for the significant water regime by variety interaction. The drought stress was much milder in 1996 than in 1995 and 1997. This, in part, explains why the drought-stressed plants yielded best in 1996. In 1996,

DK888, the top yielder, produced almost the same grain yield under drought stress and continuous irrigation. Unfavourable weather conditions shortly after silking (low irradiation in combination with relatively high temperature) seemed to limit the grain yield of well-watered DK888.

Drought increased the shoot N concentration and the N harvest index and decreased the total amount of shoot N and the apparent fertilizer N recovery in all the years; the effect on the N utilization efficiency varied among the years. The adverse effects of drought on total amount of shoot N increased with increasing N rate. The grain yield, the total amount of shoot N, and the shoot N concentration increased and the N utilization efficiency, the N harvest index, and the apparent fertilizer N recovery decreased as the rate of N application increased. The varieties differed significantly in shoot N concentration, N utilization efficiency, and N harvest index in all the years. However, there were several sporadic interactions, suggesting that it is impossible to generalize about the effects of drought, N rate, and variety on the indicators of N use. Selecting for high N utilization efficiency or low shoot N concentration will result in a lower concentration of protein in the grain and stover, thus reducing the dietary value of maize for protein-deficient humans and livestock. Selecting for high apparent fertilizer N recovery may result in varieties that are inefficient in absorbing N from soils low in plant-available N.

The concentrations of N, P, K, Mg, Ca, Mn, Zn, and Cu in the grains were determined. While the water regime did not affect the mineral composition of the grains in any of the years, the application of N fertilizer consistently reduced the concentrations of Ca and Zn and consistently increased the concentration of Mn in the grains. There was genotypic variation in the concentration of all the elements investigated; the top yielder, DK888, consistently had the lowest concentrations of N, P, Mg, and Cu in the grain. In some cases, variety interacted with water regime or N rate, but the interactions were inconsistent across the years. The water and N treatments had a minor impact on the ranking of the varieties. Thus, at a given site, varietal differences in the concentrations of grain N and minerals seem to be fairly stable across wide ranges of water and N supply. The varieties which differed most in the N and P concentrations (KTX2602 and DK888) had about the same endosperm-to-germ dry weight ratio. While the study showed that the concentrations of grain minerals are well buffered and remain stable even when the grain yield increases markedly as a result of water and N fertilizer applications, it must still be determined whether higher grain yields, as a result of breeding progress, lowers the levels of

grain minerals and protein.

It is concluded that selecting for high N utilization efficiency alone is not a promising route to developing nutritious maize in tropical countries. Since there are indications that breeding for drought tolerance simultaneously improves the potential yield of genotypes under low N, it might be wise to focus on drought tolerance only.

2. INTRODUCTION

2.1. General Introduction

Of the three main cereal-grain crops of the sub-humid to semi-arid tropics (maize, sorghum, pearl millet), maize (*Zea mays* L.) produces the highest yields when water is abundant and soil fertility is high, but maize is the least tolerant to stress (Muchow, 1989). Maize has been replaced traditionally by sorghum and pearl millet as seasonal rainfall falls below 600 mm. However, for socioeconomic reasons and due to the development of short-season maize varieties and because maize grain is better protected from birds, maize production has expanded in the semi-arid tropics (Carberry et al., 1989).

In South East Asia, maize is often grown in drought-prone and marginal areas with low soil fertility. About 50% of tropical lowland maize grown in South East Asia is reported to suffer a substantial reduction in grain yield because of periodic drought stress and low N supply (CIMMYT, 1994). According to estimates of CIMMYT (International Maize and Wheat Improvement Centre) regarding abiotic stresses, the most significant causes of yield loss on farmers' fields are low fertility (predominantly N deficiency) followed by drought and, less important, by plant competition related to low planting densities, weeds and intercrops (Edmeades and Deutsch, 1994). Both mineral and organic fertilizers are expensive or unavailable. Similarly, maize fields are usually not irrigated, because water is scarce or is used for crops of greater economic importance. Production strategies of farmers to minimize yield reductions in semi-arid tropics are: to choose maize varieties with appropriate growth duration and to plant them at a time when water deficit is least likely to occur during the late vegetative, flowering and grain filling stages (Abrecht and Carberry, 1993). Other than that mentioned, the only affordable option for many small farmers may be the cultivation of drought-tolerant and N use efficient varieties (Bolaños and Edmeades, 1993a).

CIMMYT proposes a 'reality check' to estimate the potential for increasing maize yield in drought-prone areas: About 20% of the yield gap between actual yields under drought and yield potential as determined by radiation and temperature (Muchow, 2000) can probably be closed by breeding. Another 20% can be met by innovative water conservation practices. The remaining 60% will simply have to be counteracted with additional water supply.

Maize in Thailand

The contribution of the Thai agriculture sector to the Gross Domestic Product declined from 39.4% in 1961 to 11% in 2000, due primarily to the rapid expansion of the other economic sectors (Central Intelligence Agency, 2000). In recent years, the share of agriculture in the domestic economy stabilized thanks to growing production and increasing exports. Agriculture is still considered to be an important part of the Thai economy and will remain so for years to come (National Identity Office, 1997). The planting area of maize ranks second in total area, after rice and before cassava, and covered about 1.2 million ha out of a total of 20 million ha of arable and permanent crop land. In the early 1990s, the average maize yield of 2.6 t ha⁻¹ in Thailand was relatively high for Southeast Asia and reflected the widespread use of improved varieties and agronomic practices (Dowswell et al., 1996). In recent years, the UN Food and Agriculture Organization (FAO) has reported that more maize has been produced on a smaller area (in 1995: 1,263,000 ha, in 2002: 1,134,000 ha) and that the average grain yield has risen to 3.7 t ha⁻¹ (Food and Agriculture Organization, 2003). Maize has been the only cereal crop in Thailand to increase its productivity so quickly in recent years. Main abiotic production limitations are low soil fertility and inadequate water availability. Maize in Thailand is used mainly for animal feed and grain export. An increasing domestic demand for the production of pork, beef, and poultry reduced the quantity of the exported maize and led to a steady intensification of the production of maize. Maize as food for humans is mainly sweet corn, pop corn, and baby corn; the latter is an important export product.

In most regions of Thailand, maize is usually planted on rain-fed fields at the onset of the rainy season in April or May (Kitbamroong and Chantachum, 1992). Due to the relatively long rainy season from April to October, farmers often grow two crops per season using various rotation patterns, e.g. legumes and maize, maize and maize, or maize and sorghum. The amount and distribution of rainfall is erratic; some production areas have moderate to severe drought every year. According to Manupccrapan et al. (1997), the maize area affected by drought varied from 3 to 22% of the total area sown with maize during the last 20 years (equivalent to an economic loss of about 10 to 80 million US dollars). Compared to the rest of Asia, Thailand has one of the highest proportions of farmers using improved maize germplasm on one hand and one of the lowest proportions of farmers using chemical fertilizer on the other. According to Attanandana and Yost (2003), farmers apply N fertilizer from 19 to 69 kg ha⁻¹. The high cost of fertilizer relative to the price of maize as well as inappropriate recommendations for fertilizer use may be

the main reasons for the poor adoption of fertilizers in Thailand (Harrington et al., 1991). About half the farmers apply N fertilizer to maize and of those, most apply sub-optimal amounts. Research data have, however, consistently shown that the application of N fertilizer is profitable for farmers (Dowswell et al., 1996). Estimates of the percentage of farmers planting hybrids vary between 25 and 50% (Dowswell et al., 1996). Hybrid seed is produced predominantly by private seed companies. They rely heavily, however, on germplasm provided by the public sector. Two public agencies are involved in the development and production of improved populations, open-pollinated varieties and inbred lines: the Department of Agriculture and the National Corn and Sorghum Research Centre, Farm Suwan, Kasetsart University. The principal soil groups in the central plains and in the northern and northeastern regions are reddish brown laterites and black soil types.

2.2. Drought Stress

The terminology with regard to drought stress and crops is not yet satisfactorily defined, which is a prerequisite for developing efficient breeding strategies for improving drought tolerance or for a physiological treatise about drought resistance (Belhassen, 1997). Levitt (1980) suggests that the term 'drought resistance' should include both 'tolerance' and 'avoidance' mechanisms. Some authors prefer the term 'dehydration' to 'drought' and consequently refer to 'dehydration tolerance' (Boyer, 1996; Turner, 2002). Drought tolerance can also be described by referring to resource economics. Passioura (1996) stated that three principal physiological factors are involved in the 'most effective use' of water as a resource to produce grain: water uptake, water use efficiency (WUE), and harvest index (see below). He argues that these components are independent of each other and that an increase in any one of them is likely to increase yield. In this work, 'drought' and 'drought tolerance' are used in terms of yield in relation to a limited supply of water. Plants with better growth under limited water supply are considered to be drought-tolerant, regardless of how the improvement in growth occurs, or whether the WUE is affected, in agreement with Boyer (1996).

Forms of drought stress

There are several periods, during which drought stress can affect the growth and yield of maize to a varying extent: the stages of seedling establishment, vegetative or post-emergence growth,

flowering or reproduction, and grain filling. It is generally accepted that drought stress in the period bracketing flowering affects grain yield most severely (Grant et al., 1989; Herrero and Johnson, 1981; Westgate and Thomson Grant, 1989).

In the tropical rainy season (uni- and bimodal), the probability of drought is highest at the beginning and end of the growing seasons; it also depends on the duration of the rainy season and the cropping pattern. Many farmers choose the planting date so that the period of the most intensive rainfalls coincides with the anthesis of the maize crop. Whereas the complete loss of a crop due to drought stress during emergence may be countered by planting a second crop, unfavourable growth conditions during later growth stages will inevitably lead to substantial yield losses.

Stress phenology and physiology

The severity and time of the stress in relation to the growth stage of the crop must be considered in breeding programmes and research projects (Lorens et al., 1987b). Passioura (1996) emphasized that the main developmental changes in the crop (e.g. floral initiation, flowering, rate of development of leaf area) must match the pattern of water supply in relation to evaporative demand. In general, it is important that the type of drought stress and the target environment, under which a variety realizes a higher yield, be considered. Experience gained under Mediterranean conditions (terminal drought stress), when short-season varieties are planted so as to avoid the late-season stress and, thus, produce higher yields, cannot be applied to mid-season drought stress. Late-flowering varieties may recover better from mid-season stress; a longer growth period is often associated with more intensive root growth and, hence, the extraction of soil moisture from deeper layers (Matthews et al., 1990). Turner (2002) concludes that, in environments with varying drought stress, it may be preferable to breed for phenological plasticity to enable genotypes to profit from favourable growth periods. Another possibility is to select genotypes with intermediate life cycles but with some dehydration tolerance. This would enable them not only to escape late drought stress in average seasons, but also to survive occasional, drier-than-average seasons.

a) Effects of pre-anthesis drought: If water is limited during vegetative growth, the final leaf area will be smaller and, thus, carbon gain will be reduced throughout the growing season (Nilson and Orcutt, 1996). Furthermore, the process of storage of reserves in the stem and ear shank is affected mainly by the conditions under which assimilation takes place before flowering.

Prolonged drought stress during the vegetative stages affects the length of the internodes by influencing the cell size development and, thus, the capacity for storing assimilates (Denmead and Shaw, 1960). Under favourable conditions (no drought stress), reserves contribute little to reproductive success (Schussler and Westgate, 1995). However, when photosynthesis is limited during grain filling, the remobilisation of stem reserves is considered to be a main source of carbohydrates for grain filling (Blum, 1996). The immediate impact of a water deficit on the effective leaf area (smaller leaf area as a result of leaf rolling) largely determines the extent of assimilation under drought (Blum, 1997). Plasticity in leaf area development is an important strategy of a drought-stressed crop for maintaining control over water use (Blum, 1996).

b) Effects of drought stress during reproductive stage: Abortion of ovules, kernels, and ears occurs from one week before silking to two weeks after silking. Drought, shade, high density, and/or N deficiency stress during this period accentuate these processes (Uhart and Andrade, 1995). From various studies, Andrade et al. (2000) suggest that water and/or N deficiency reduce carbon availability and dry matter (DM) partitioning to the ear during the critical period that determines grain number. Unfavourable environmental conditions can cause a reduction in the number of kernels per plant (Fischer and Palmer, 1984; Kiniry and Ritchie, 1985). It is generally accepted that, when drought begins to affect the plant during reproduction, the plant decreases the reproductive demand for carbon by reducing the number or size of the sinks. Consequently, tillers may degenerate, flowers drop, pollen die, and ovules abort (Blum, 1996). The maize plant inherently produces many more potential ears, ovules, and kernels than the number that reach maturity (Tollenaar, 1977). Ovule abortion can occur when ovules fail to extrude silks because of slow growth rates, whereas kernels abort following pollination. Westgate and Boyer (1986) observed that a low water potential during anthesis does not hinder pollination, but prevents the development of embryos due to a lack of photosynthates. When the supply of assimilates to the ear falls below the threshold necessary for ovules to develop, all the kernels abort, resulting in a barren plant (Edmeades et al., 1993). To analyse the factors, affecting kernel development and, ultimately, grain yield, both the number and size of the kernels should be considered, because their existence is determined at different stages of the crop's life cycle (Banziger et al., 1999).

Anthesis-silking interval

If drought occurs during the reproductive stages of maize silking is considerably delayed, while anthesis is delayed to a lesser extent. Thus, the anthesis-silking interval (days from anthesis to

silking; ASI) increases, which may be an important reason for crop failure under drought stress, since this trait is highly correlated with kernel set (Byrne et al., 1995). Results of trials with temperate hybrids suggest that direct effects of insufficient pollen supply on grain number per plant occur only when pollen production is reduced by 80% and more or when the ASI exceeds eight days (Bassetti and Westgate, 1994). Edmcades et al. (2000) concluded that the ASI is a good and easily ascertainable external indicator of: partitioning of currently produced assimilates to the ear, the growth rate of the female spikelet, grain number, and perhaps of the water potential of the plant (see '2.4. Breeding'). This seems to be true with regard to the partitioning of assimilates to the ear under low N, too.

Roots

A well developed root system as a constitutive trait is favourable in many environments. It enables the plant to make better use of water and minerals and is an important component of drought tolerance at different growth stages (Blum, 1996; Weerathaworn et al., 1992a). The potential quantity of accumulated water depends on the extent of root proliferation in the soil volume. Patterns of resource allocation change when water is limited: root tissues tend to grow more than the leaf tissues. When drought stress occurs during early growth stages the root/shoot ratio changes considerably (Nielsen and Hinkle, 1996) and usually increases (Sharp and Davies, 1989). A longer phase of growth of late genotypes is associated with greater biomass, both above and below ground; this leads to higher root length density in the soil and, consequently, a greater potential productivity (Blum, 1996). According to Anderson (1987), the most rapid root development occurs during the first eight weeks after planting. The same author also found that, when rainfall is adequate, the root system of maize formed during the first 60 days can sustain the plant until harvest; on the other hand, when soil moisture is limited, root growth may last throughout the growing season, even when N fertilization is inadequate. In contrast, Bruce et al. (2002) assumed that vigorous root growth occurs at the expense of grain production, despite the advantage of improved water acquisition in dry soils. Increases in grain yield under drought, resulting from selection for drought tolerance, are associated with a smaller root biomass in the upper 50 cm of the root profile in a tropical maize population (Bolaños et al., 1993). Recent research at CIMMYT has investigated the possibility of measuring the root capacitance to assess the absorptive area of the roots and to use this as a selection parameter for enhanced drought tolerance. Special emphasis has been placed on determining whether a greater number of brace roots and the extensive development of fine roots (both indicated by a large capacitance) favour

the formation of above-ground biomass (Edmeades et al., 2000).

Water use efficiency

Water use efficiency (WUE) is the total above-ground DM produced by plants per unit of water used. The WUE of a crop does not change as the availability of water varies. However, it may differ among species, climates, and from year to year; furthermore, it may depend on the availability of different mineral nutrients (Boyer, 1996). Because of diminishing water reserves and salt-degraded soils in the USA, the establishment of new irrigation schemes has proved to be less profitable than in the past. This has increased the interest in enhancing the efficiency of water use in irrigation systems and in improving the crop performance on rain-fed land (Boyer, 1996). Various authors have pointed out that drought tolerance and WUE are not synonymous. Genotypes with a higher WUE use the most water and may, therefore, be less productive when there are prolonged periods of dry weather. Thus, the selection of drought-tolerant crops for a higher WUE alone might be counter-productive (Matthews et al., 1990). Further restrictions of selection for WUE in drought tolerance selection programmes are discussed under chapter 'Breeding for Drought Tolerance' (2.4.1.).

Harvest index

There has been a general increase in the yields of modern crops, with little change in the total above-ground biomass. This improvement is, therefore, attributed to an increase in the harvest index (HI). The increase occurred with little change in the amount of water used, resulting in a natural increase in the WUE with respect to grain yield (Richards et al., 1993). The HI of temperate maize cultivars is often above 0.5 (Costa et al., 2002), whereas much lower values have been reported for tropical lowland maize (Feil et al., 1992b). Standard programmes for improving tropical and subtropical maize over the last decades resulted in a reduced plant height and an increase in the HI from about 0.3 to 0.45 (Dowswell et al., 1996). Tollenaar and Wu (1999), however, showed for temperate (Ontario) maize hybrids that a reported increase in HI was not found when old and new hybrids, resulting from three decades of breeding for yield improvement, were planted at their specific optimal plant densities. They concluded that most of the genetic improvement in yield is attributed to greater stress tolerance. Sinclair et al. (1990) reported that a decrease in grain yield under moderate drought stress is proportional to the decrease in the accumulated biomass; the HI remained the same. The HI decreased, however, under severe water deficit, when the accumulated biomass was less than about 1100 g m⁻². Under extreme, artificial

water deficits, the HI can decrease to as low as zero (Boyle et al., 1991). Experiments with sorghum (*Sorghum bicolor* L. Moench), grown on stored soil water, showed an overall better grain yield of the hybrids compared to the open-pollinated varieties (OPV). This was attributed mainly to the fact that the HI of the hybrids was more than twice as high as that of the OPVs. In terms of the plant water status and mean daily biomass production, however, the OPVs were more drought-tolerant than the hybrids (Blum et al., 1992). Blum suggested breeding for a higher potential HI of the OPVs. Siri (1993) observed that drought during the vegetative stage of tropical maize led to a higher HI (about 24%) with large genotypic variation.

Plant water status

Physiological traits such as higher leaf water potential, osmotic adjustment, and cooler leaves were associated with superior yield under water limited conditions (Nilson and Orcutt, 1996; Petrie and Hall, 1992; Richards, 1989). Some authors noted that the short-term response of plants to changes in water status – including physiological, biochemical, and molecular changes associated with desiccation tolerance – may not be the most desirable traits for manipulation to increase the yield potential of crops under water deficit (Blum, 1996; Passioura, 1996).

2.3. Nitrogen Deficiency

General

The main agricultural soils in the semi-arid regions are low in N, and the poor availability of N for plant uptake seriously limits productivity (Muchow, 1988b). In many of the poorest regions, chemical fertilizer is unavailable or the cost is prohibitive (Edmeades and Deutsch, 1994). Maize cultivars that are productive under conditions of low N availability are, thus, highly desirable (Sallah et al., 1996).

Effect of nitrogen fertilization on grain yield

There are numerous publications dealing with the impact of N fertilization on grain yield, biomass yield, and yield components. Oikeh (1999) conducted experiments with rain-fed maize in the Nigerian savanna. Grain yield, total biomass, and HI increased as the rate of N fertilizer increased. In contrast, the HI was not related to the level of N fertilization in an experiment in Australia (Pearson and Jacobs, 1987). Averaged over 28 experiments conducted in Missouri,

Scharf et al. (2002) reported that there was no evidence of yield reduction when N applications were delayed even by the V11 stage; there seemed to be small yield reductions (3%) when applications were delayed until V12 to V16, and moderate yield reductions (15%) when applications were delayed until silking. Side-dress applications of N led to visible N stress but did not necessarily cause a reduction in grain yield compared to pre-plant N applications. Thus, it was concluded that the time of N fertilization is not critical in terms of grain yield. Experiments on a sandy soil under semi-arid conditions, however, have shown that the yields were highest when all the N fertilizer was applied less than three weeks after planting. It was postulated that the stimulating effect of adequate N supply on early root growth is of paramount importance for soil moisture utilization under limited precipitation conditions (Adriaanse and Human, 1993). Results presented by Blumenthal et al. (2003) suggest that the optimum population density does not depend on the rate of N application. If this were so, it would be unnecessary to adapt the level of N supply to the plant density.

Physiology

The morphological and physiological responses of maize to a continuous N deficit include smaller plants, reduced radiation use efficiency, accelerated leaf senescence, increased mobilization of vegetative N to the grain, and a lower plant N concentration (Muchow and Davis, 1988). According to Presterl et al. (2002), N-deficiency stress delays shoot elongation and leaf growth, but increases root growth. Under high N supply, uptake depends mainly on the growth-related demand for N, whereas under low N, uptake depends on morphological and physiological characteristics.

Reproductive structures

In a field experiment, in which heavy N fertilization enhanced grain yield compared to the unfertilized control, the application of N did not affect the number of spikelets per ear. However, the number of grains that developed from the spikelets of fertilized plants was higher (Lemcoff and Loomis, 1986). The effect of N application on kernel weight was not significant. In contrast, in an experiment in Nigeria, Oikeh et al. (1998) found that the grain weight increased as the level of N fertilization increased. Similar results were obtained in Niger by Pandey et al. (2000). Here, an increase in the rate of N fertilizer also increased the number of kernels m^{-2} ; both the number of ears m^{-2} as well as the number of grain per ear increased, too. In the study of Costa et al. (2002), the application of N fertilizer significantly increased the length and diameter of the ears

in three of four year-sites. In contrast, N did not affect the number of kernel rows or the kernel number per row. According to Anderson et al. (1984), increasing the rate of N application tended to increase the number of ears per plant of prolific and semi-prolific cultivars.

Nitrogen remobilisation

Remobilisation of N from stalks and leaves may be an important source of N for deposition in the grain (Hanway, 1962). There are, however, contrasting reports about the importance of N remobilisation. Likewise, the findings reported on the timing of remobilisation are inconsistent. Anderson et al. (1984) concluded that this variation in N remobilisation may be due to environmental or genotypic differences or to their interaction. Muchow (1988b) found that translocation of pre-anthesis assimilates to grain occurs when there is a water deficit at high N supply as well as under adequate irrigation at low-N supply. Little information is available, however, on the mobilization of N and assimilates under simultaneous drought stress and N deficiency (Muchow, 1990).

Because maize evolved in the tropics where N is inherently deficient, natural selection has favoured the early uptake of N from the soil, its storage in leaves as photosynthetic enzymes, and its subsequent remobilisation to the developing grain during grain filling (Bruce et al., 2002). Nitrogen accumulation in the grain decreases under both drought and N stress (Bennett et al., 1989); thus, the demand for N by the growing ear is met by the remobilisation of N from the leaves and stem. When the grain sink size increases due to selection for grain yield, then this may accelerate foliar senescence. In dry soils in particular, the demands for N by the grain may exceed the plant's capacity for uptake (Bruce et al., 2002). It appears that delayed leaf senescence contributes to larger biomass gains under severe N stress (Banziger et al., 1999).

Flowering

The flowering of tropical maize is generally delayed by N deficit. This may be appropriate in rain-fed environments where maize is cultivated, in that an extended period for nutrient acquisition might assist in exploiting the erratic, multi-modal pattern of N availability that is common in the tropics (Gutschik, 1981). Grain yield was found to be positively associated with shoot biomass and N content at anthesis under conditions of N deficiency (Muchow, 1988b). It was shown that differences in leaf N affected radiation use efficiency and, thus, biomass production. Plant height of N stressed plants has been shown to be a good indicator of biomass at anthesis (Lafitte and Edmeades, 1988).

Roots

Findings of studies of the effects of N availability on root growth are conflicting; both increased and decreased corn root length have been observed in response to N fertilization. In a field experiment, Anderson (1987) found an increase in total root length and weight and a decrease in root diameter in two of three years with N fertilization. Eghball and Maranville (1993) showed that N fertilization slowed down root growth. They assumed that a smaller root mass, associated with greater N availability, limits root penetration and, hence, reduces nutrient and water extraction from the soil.

Durieux et al. (1994) reported that the root weight of mature field-grown maize declined as the rate of N application declined, but there were no significant effects of N application at two earlier sampling dates, namely 20 days before silking and at silking. Oikeh et al. (1999) studied the growth and distribution of rain-fed maize roots in the field and found that root growth was more extensive under moderate N supply than under zero N and high N supply, particularly in the sub-soil. During periods of limited water availability, the flow of N from the roots to the leaves decelerates; and higher concentrations of nitrate and ammonium build up in drought-stressed roots than in the roots of well-watered plants. The higher concentration of nitrogenous ions in the roots inhibits the absorption of N from the soil (Nielsen and Hinkle, 1996).

Water by nitrogen interaction

Many studies about the effect of N supply on plant productivity were conducted under fully-irrigated conditions to avoid the confounding influences of differences in water supply (Muchow, 1988a). Comparatively few studies have focused on the interactive effects of N fertilization and irrigation. Variability in the response to N fertilization may be due to erratic rainfalls and/or low water-holding capacity (Muchow, 1988a). The application of N fertilizer to drought-stressed plants seems to have a positive effect on maize yield (Boyer, 1996; Eck, 1984). In a one-year field experiment in Nebraska of Eghball and Maranville (1991), there were significant water regime by cultivar and cultivar by N interactions but no significant three-way interactions. There were, however, no significant effects on total shoot N (TSN) and grain N. The authors compared furrow-irrigated maize with rain-fed maize, the latter of which was subjected to drought stress throughout most of the growing season. Averaged across four cultivars and four rates of N application, furrow irrigation increased the TSN by maturity by 20%, grain N by 29%, and grain yield by 43% compared to rain-fed maize; thus, grain yield was more responsive to irrigation than

the N-related parameters. It is possible, however, that the effects of water regime and plant density might have been confounded, since the plant densities were not the same under rain-fed conditions and irrigation.

Pandey et al. (2000) conducted experiments in Niger with five levels of N fertilization and five irrigation regimes. They found that the effect of drought on kernel number m^{-2} depended strongly on the irrigation regime. Drought stress during the vegetative stage did not reduce the kernel number relative to the well-irrigated control, but the reduction in kernel number was as high as almost 50% when the maize was subjected to permanent drought. Nitrogen use modified water use at all irrigation levels, in the sense that relative yield reduction due to a water shortage was much more severe at high N rates. Absolute grain yields were highest at a rate of 120 kg N ha^{-1} and less under 160 kg N ha^{-1} , irrespective of the form of drought stress applied. Similar observations were made by Burman et al. (1962) who, in an experiment in Wyoming, found that 70 kg N ha^{-1} were sufficient for maximum yield under drought stress while the grain yield response to N fertilization was more pronounced when observed drought stress was less severe. In Utah, the DM yield of drought-stressed decreased at N rates exceeding 200 kg N ha^{-1} (Bauder et al., 1975). In Nebraska, the grain yield of well-irrigated maize increased as the rate of N application increased. Under drought stress, however, maximum grain yield was obtained at 120 kg N ha^{-1} ; at 180 kg N ha^{-1} the grain yield even decreased (Eghball and Maranville, 1991). In Florida, drought stress during vegetative stages of development did not reduce the grain yield under low (116 kg N ha^{-1}) N fertilization. The grain yield decreased, however, under high (401 kg N ha^{-1}) N fertilization, and was 19% lower than under ample water supply. More severe drought stress brought about yield depressions of 51% (low N) and 75% (high N). Under severe drought, N fertilization tended to cause a decrease in grain yield. Eck (1984) investigated the response of maize grain yield to increasing rates of N application under various drought stress scenarios. He found a statistically significant N rate x irrigation regime interaction. Adequate amounts of N fertilizer led to a slight increase in grain yield under drought stress and a strong increase in grain yield at ample water supply. Excessive N fertilization did not reduce grain yield even under severe drought stress. Eghball and Maranville (1991) also found significant effects of water regime by cultivar, water regime by N rate, and N rate by cultivar interactions on grain yield but significant three-way interactions did not occur. The interactions had no significant effects on total shoot N and grain N.

Knipf and Mason (1989) reported significant effects of water regime x N fertilization on grain yield, grain protein concentration, and lysine concentration in the grain of maize in Nebraska, whereas the effect of this interaction on the lysine concentration in protein was not significant. The study included four hybrids that differed in maturity rating (short season vs. long season cultivars) and grain quality (two *opaque-2* vs. two normal cultivars). The hybrid by water regime by N fertilization interaction did not have a significant effect on any of the parameters investigated.

Effect of nitrogen fertilization on selected nitrogen parameters

The total N content of the above-ground biomass and the grain N yield usually increase with increasing rate of N fertilization (Eghball and Maranville, 1991). Pearson and Jacobs (1987) found a linear relationship between the rate of N application and the TSN in an experiment on coarse sand in Australia, with N rates ranging from 45 to 173 kg N ha⁻¹. There is broad environmental variation in the proportion of grain N to total above-ground N at harvest ('nitrogen harvest index'; NHI). For example, Feil et al. (1990) found large differences in the mean NHI between two experiments conducted during a rainy (0.52) and a dry (0.69) season in Thailand. The NHI is usually hardly affected by the extent of N fertilization. For example, in the experiment of Pearson and Jacobs (1987), N supply and NHI were not related; the average NHI was 0.66. However, in the study of Anderson et al. (1984), a heavy N fertilizer dressing reduced the NHI from 0.73 (at 56 kg N ha⁻¹) to 0.66 (at 224 kg N ha⁻¹). From the data presented by Eghball and Maranville (1991) it can be calculated that an increase in the rate of N application from 0 to 120 kg N ha⁻¹ had only a slight effect on the NHI, whereas 180 kg N ha⁻¹ reduced the NHI from about 0.74 to 0.67. Relatively little information has been published about cultivar differences in the NHI of maize. A long-term selection programme for grain N concentration was conducted at the University of Illinois. After 87 generations of selection, the low-protein strain had an NHI of 0.4, while the strain selected for high grain protein concentration had an NHI of 0.62 (Wyss et al., 1991). In an experiment in Germany, Zink and Michael (1985) found an NHI of 0.72 for a normal hybrid and 0.75 for a protein-rich hybrid. From the data presented by Eghball and Maranville (1991) the mean NHIs of the four cultivars tested in Nebraska were calculated and varied from 0.67 to 0.79. In a set of 12 tropical cultivars (OPVs and hybrids) grown on Farm Suwan during two cropping seasons and under three rates of N application, the mean NHI of the cultivars ranged from 0.57 to 0.67 (Feil et al., 1990). In an earlier experiment, which was conducted at the same

site in the rainy season, the NHI of tropical cultivars varied between 0.48 and 0.60 (Thiraporn et al., 1983).

Improving the N use efficiency (NUE) of maize would especially benefit many developing countries, where yields are low and fertilizer application inadequate (Akintoye et al., 1999; Cassman et al., 2003; Muruli and Paulsen, 1981). Nitrogen use efficiency has been described in various ways. According to Sattelmacher et al. (1994), NUE is the ability of a genotype to produce superior grain yields under low N in the soil in comparison with other genotypes. Moll et al. (1982) defined the NUE as grain production per unit N available in the soil and distinguished two primary components of NUE: (i) the efficiency of N absorption from the soil, the N uptake efficiency, defined as unit grain weight per unit soil N; and (ii) the efficiency with which the absorbed N is utilized to produce grain, the N utilization efficiency (NUE), defined as unit grain weight per unit shoot N. Moll et al. (1982) investigated the contribution of N uptake and utilization processes to the variation in NUE. They found that, at low N supply, differences in the NUE were due largely to variation in utilization of accumulated N, but at high N supply, they were due mainly to variation in the uptake efficiency. Nutrient uptake is related to root mass, biochemical and physiological mechanisms involved in nitrate assimilation, and energy supply (Akintoye et al., 1999). Continuous N uptake during the grain-filling period has been associated with the ability to maintain root growth after silking, which may be a function of assimilate supply. Pre-anthesis drought may influence the patterns of N uptake and partitioning before flowering, both of which are critical for maintaining grain number in N-limited environments (Pearson and Jacobs, 1987). Muruli and Paulsen (1981) found that about 40% of grain N came from the soil and roots after pollination.

Since the amount of plant-available soil N is difficult to measure accurately, several investigators determined the effects of N fertilization and variety on the NUE of maize. The NUE has also been defined as the ratio of shoot biomass to TSN (Eghball and Maranville, 1991). In that study, the NUE decreased with the increasing availability of N to the plants. Anderson et al. (1985) found significant genotypic variation in the NUE and showed that it and the N uptake efficiency are related to the degree of prolificacy. An increase in N uptake in association with increased prolificacy has been reported by several authors (Anderson et al., 1984; Pan et al., 1995). Machado and Fernandes (2001) reported significant variation in the NUE of Brazilian varieties. Lafitte et al. (1997) determined the NUE of tropical landraces and improved varieties and found

that the NUtE of the improved varieties was clearly higher, irrespective of the level of N supply. In the field experiments of Eghball and Maranville (1991), the NUtE was not significantly affected by the water regime and the water regime by cultivar interaction. However, Bennett et al. (1989) found that, under high N, drought stress reduced the NUtE.

The apparent recovery of fertilizer N (AFNR) – here defined as the difference between N accumulation, with and without N application, divided by the amount of N applied – usually diminishes as the rate of N application increases. Feil (1994) conducted a field experiment with 12 tropic cultivars (OPVs and hybrids) on Farm Suwan and found average N fertilizer recovery rates of 65.1 and 59.3% at 40 and 80 kg N ha⁻¹, respectively. In another experiment, carried out at the same site and with 16 cultivars (OPVs and hybrids), recovery rates of 62.4%, 58.7%, and 44.3% were observed at 40, 80, and 160 kg N ha⁻¹, respectively (Feil et al., 1993).

Grain nitrogen concentration

In contrast to wheat, only few studies have dealt with the yield - protein relationship in maize (Feil, 1997). Some researchers found that the grain yield and grain protein concentrations are inversely related (Dudley et al., 1977; Gupta et al., 1975), while others found either a weak negative or no relationship between productivity and the protein level (Beauchamp et al., 1976; Eberhard, 1977; Feil et al., 1993; Feil et al., 1990; Pixley and Bjarnason, 1993; Pollmer et al., 1979; Tsai et al., 1992). According to Duvick and Cassmann (1999), the grain yield of US maize cultivars has increased linearly since 1930 when grown at moderate to high plant densities, but there was no increase in the grain yield at extremely low plant density. Averaged across the plant densities, there was a significant decline in the grain protein concentration.

Jurgens et al. (1978) found that maize under drought stress during grain filling produced a lower grain yield than the control but had a higher percentage of N in the grain. This was confirmed by Harder et al. (1982), who subjected maize to drought stress near silking and during grain filling. They also reported that the drought stress did not alter the concentrations of phosphorus (P) and potassium (K) in the grain. Kniep and Mason (1989) compared quality traits of furrow-irrigated and rain-fed maize in Nebraska and found that drought stress decreased grain yield and increased the grain protein concentration. The concentration of lysine in the protein decreased, whereas the concentration of lysine in the grain DM increased. Similar results were obtained by Hancock et al. (1988).

In most experiments, the concentration of grain protein increased as the rate of N application

increased (Bennett et al., 1953; Feil et al., 1992a; Kniep and Mason, 1989; Oikeh et al., 1998; Pierre et al., 1977; Thiraporn et al., 1992; Tsai et al., 1992). In some cases, however, fertilization of N had a slight effect or even lowered the grain percentage (Cerrato and Blackmer, 1990; Meisinger et al., 1985). The number of contrasting findings can be reduced to a fundamental curve, which describes the response of the grain N concentration to an increasing rate of N application (Feil and Stamp, 1993). The odd shape of this curve is the result of two processes: (i) deposition of protein in the grain and (ii) dilution of grain protein by other grain components, mainly carbohydrates. On soils with low N mineralization, low rates of N fertilizer will boost both the grain protein yield and grain yield. The increments in grain yield are greater than those in the grain protein yield, which causes a decrease in the protein concentration (i.e. the ratio of grain protein to grain yield). With high rates of N application, however, gains in the grain protein yield exceed those in grain yield, leading to an increase in the grain protein concentration.

Grain protein quality

Ordinary maize protein is of poor nutritional quality for humans and non-ruminant livestock, because it is low in lysine and tryptophan and has an undesirable ratio of leucine to isoleucine (Alexander, 1988). Increases in the grain protein concentration, brought about by N fertilizer, were found to decrease the concentration of lysine in the protein, whereas the grain lysine concentration increased. Independent of the hybrid type under investigation (*opaque-2* vs. normal maize), the concentrations of grain protein and grain lysine were positively correlated (Kniep and Mason, 1989).

2.4. Breeding

2.4.1. Breeding for Drought Tolerance

The time and the intensity of drought is unpredictable and varies from year to year. This makes breeding for drought tolerance particularly slow and difficult, whether breeding for the selection of improved grain yield or for the identification of important selection traits (Richards, 1996). Several factors have changed the focus of maize geneticists and breeders in programmes for improving maize for drought-prone environments: (a) the lack of control over stress conditions; (b) yields that are too low or too high to be useful for selection when trials take place in uncontrolled, drought-prone environments; (c) high error variances that are normal when testing

in drought-stress environments; (d) high genotype by environment interactions resulting from variations in rainfall and temperature, from location to location and from year to year, or from different characteristic of genotypes; and (e) the apparent negative correlation between drought resistance and yield potential of a hybrid under better growth conditions (Jensen and Cavalieri, 1983).

There are, however, some promising findings which suggest that there may be ways to overcome the above problems. To point (c) : The experiments described by Jensen and Cavalieri (1983) showed that improvement of maize genotypes under limited water availability need not sacrifice yield gains under more favourable conditions. (d): Because the effect of dry conditions on yield varies depending on the developmental stage at which drought occurs, it is important that the timing and the intensity of the imposed drought stress in breeding programmes are similar to the typical droughts in the target environment (Lorens et al., 1987b). (e): Actual yield under moderate drought reflects better the yield potential of a genotype, before the stress is severe enough to induce a genotype x environment interaction for yield (Richards, 1989). Jensen and Cavalieri (1983) found in large-scale experiments in the Southern USA an overall correlation of $r=0.37$ between mean hybrid grain yield and the phenotypical yield stability of a given hybrid against the mean yield of all hybrids at the same location. Thus, selection for high yield and drought tolerance may be feasible.

CIMMYT

El Centro Internacional de Mejoramiento de Maíz y Trigo (CIMMYT) is a non-profit organization with headquarters in Mexico and 17 regional offices worldwide, mainly in developing countries. CIMMYT conducts research into maize and wheat and provides a broad array of high-yielding maize varietics, hybrids, and inbred lines for non-temperate regions which can tolerate major environmental stresses such as infertile soil, drought, insect pests, and diseases. The centre initiated breeding for drought-tolerant maize in 1975 which made such progress that selection for this trait has become routine for improving maize germplasm. Progenies are typically evaluated in replicated trials at one or two levels of drought stress by recurrent selection during a rain-free period. At the same time, progenies are tested under well-watered conditions (irrigation) for their potential yield and competitiveness in a wet year (Heisey and Edmeades, 1999). Drought is imposed during flowering and grain filling so that the average grain yield is reduced to 30 to 60% (intermediate stress level, during grain-filling) or 15 to 30% (severe stress level, during flowering and grain-filling), respectively, of unstressed yields (Banziger, 1999). The

selection is based on an index that seeks to reflect to what extent a line is able to maintain the time from sowing to anthesis, maintain or increase grain yield under well-watered conditions, increase grain yield under drought, and decrease ASI, barrenness, the rate of leaf senescence, and leaf rolling under drought. Selection gains were largely the result of reduced barrenness and an increase in the HI (Banziger et al., 2000; Bolaños and Edmeades, 1993a, b; Passioura, 1996). Drought-tolerant populations of CIMMYT composites from numerous landraces and cultivars, with one or several drought-adaptive traits, were competitive over the full range of water availability. However, they showed some inherited agronomic defects, which limits the scope of such approaches, mainly from an economic perspective and for national breeding programmes (Edmeades et al., 2000). It is, therefore, recommended that recurrent selection with elite germplasm be implemented to achieve the most rapid improvement in tolerance to drought.

Selection strategies and criteria

Breeding for drought tolerance requires well-managed water regimes in terms of timing, intensity, and uniformity. Only then will selection results be comparable and significant and ultimately lead to breeding progress. When selecting for drought tolerance, different water regimes serve different purposes: Well-watered regimes enable the assessment of yield potential, phenological stages, and morphological traits under non-stress conditions. Drought stress at defined stages of development influences specific parameters. Stover biomass yield, plant height, number of leaves and leaf area, and the number of ovules and ears are determined to a large extent before anthesis. Stress at flowering reveals the genetic variation in the ASI, number of kernels, and ears through abortion, whereas post-flowering stress mainly shows the genetic variability in the kernel weight and leaf senescence (Banziger et al., 2000). Although CIMMYT assumes that 50% of yield losses worldwide are due to drought stress before flowering, stress during flowering is considered to be more important for two reasons: First, maize is particularly susceptible to drought at this stage. The grain yield can be reduced nearly to zero by severe stress during a relatively short period at flowering, when the final number of ears per plant and the number of kernels per plant are determined (Edmeades and Deutsch, 1994; Grant et al., 1989). According to Bolaños and Edmeades (1996), the ability to produce an ear under stress is the most important characteristic associated with drought tolerance. Second, at the flowering stage, the season is too far advanced to consider replanting or adjustment of cropping patterns. Blum (1997) distinguished between genes that are expressed constitutively and genes that are stress-adaptive. If stress-adaptive genes of beneficial traits exist in the breeding material, then they are expressed only when the stress is

sufficiently severe (Boyer, 1996). Selection under various water regimes generally reduces the genetic variation in the potential grain yield (Bolaños and Edmeades, 1996). Likewise, other constitutive (i.e. non-adaptive) traits such as plant phenology, early plant vigour, root size and depth, and utilization of stem reserves for grain filling, may serve as selection criteria under moderate stress only (Blum, 1996). Blum argued that the constitutive traits should be improved before the more complex, stress-adaptive genes are targeted.

Secondary traits

In addition to grain yield, it is recommended that a series of simple secondary traits be used in selecting for drought tolerance (Edmeades et al., 2000). Since heritability for grain yield declines under severe drought stress, secondary traits may increase selection efficiency when the yields fall below 50 to 60% of the potential yield (Bolaños and Edmeades, 1993b; Brucc et al., 2002). Traits that are most likely to improve yield under drought should meet several criteria: (a) The degree of influence that a trait exerts on yield depends on the period over which it is effective (Passioura, 1996). For example, a trait that influences leaf area will be more important than a trait that is linked to the stomatal response to the onset of drought. (b) The capacity of a trait to influence yield is related to the level of organization (molecule-cell-organ-plant-crop) in which the trait is primarily expressed. In general, the closer the trait is to the 'crop'-level, the more influence it will have on productivity. (c) It is crucial to know the target environment for a specific trait (i.e. seasonal rainfall pattern, soil and its water holding capacity, evapotranspiration (ET) in relevant stages). (d) Finally, desirable traits may differ substantially depending on requirements of subsistence farming or of a market-orientated agriculture (Richards, 1996). It is important for breeders to know which secondary trait, in combination with grain yield, improves breeding (Banziger et al., 2000). CIMMYT breeders found that yield under drought was closely related to the number of kernels and ears per plant and that ASI accounted most for the variation in grain yield under drought stress at flowering (Edmeades et al., 1995).

Water use efficiency

The WUE is determined mainly by the crop's potential yield. Selection for this trait under highly productive conditions may shift a population towards increased drought susceptibility (Blum, 1996). In turn, selection for high WUE under severe drought stress may not result in a higher grain yield in stress environments, since the WUE or the leaf area index (defined as the one sided green leaf area per unit ground area; LAI) might interact with the environment (Blum and

Johnson, 1992). Bolaños and Edmeades (1996) concluded that traits indicative of reproductive success explained much more of the variation in maize grain yield than traits indicative of the plant water status and WUE. Crop improvement under conditions of limited water involves more than WUE. Adaptive characteristics such as osmotic adjustment or abscisic acid (ABA) are called into play only when there is a considerable water shortage. Roots may penetrate deeper soil layers, so assimilation may persist longer during a water deficit in some genotypes than in others (Lorens et al., 1987a).

Prolificacy

In temperate germplasm, prolificacy has been associated with high grain yield under low N and often imparts greater yield stability over a range of environments, which is essential for the development of high-yielding and N-efficient hybrids (Moll et al., 1987). In breeding programmes in South Africa, prolificacy has been identified as one of the primary characteristics in the selection of maize genotypes for drought tolerance. It is argued that prolificacy combined with low plant density, thereby maintaining the same number of ears per unit area, may be a method for overcoming drought (Magson, 1996). Edmeades et al. (2000), however, emphasised that prolificacy per se contributes little to drought tolerance.

Hybrid versus open-pollinated varieties

Extensive trials conducted by CIMMYT evaluated the performance of the most prominent drought-tolerant populations and the best stress-tolerant hybrids. Stress-tolerant hybrids generally out-yielded OPVs under a wide range of conditions, and that heterosis must be considered an important source of stress tolerance (Blum, 1997). On the other hand, commercial hybrids, which are not especially stress-tolerant, compared with hybrids developed from stress-tolerant inbred lines often failed when cultivated under conditions of severe drought at flowering (Edmeades et al., 2000). Although a considerable amount of CIMMYT's research into drought tolerance has focused on OPVs, evidence suggests that improvements in drought tolerance carry over to lines and hybrids and that they are consistent across various drought scenarios (Banziger et al., 2000). According to Akintoye et al. (1999), there is no evidence that hybrids are inherently more susceptible to low soil fertility than OPVs. Breeding for genotypes with a medium yielding potential might be a more promising approach, provided that these genotypes will be used in certain environments where drought is predictable in terms of time, duration, and intensity. This was observed for sorghum by Blum et al. (1992) and for barley by Ceccarelli et al. (1992); the

latter compared barley land races with high-yielding cultivars under extreme drought stress.

2.4.2. Breeding for Tolerance to Low-Nitrogen

According to Banziger et al. (2000), breeding for low-N stress tolerance is simpler than breeding for drought tolerance, because N deficiency usually affects plant growth more evenly over time compared to random drought spells. Thus, testing lines under one level of relatively severe low-N stress should suffice to assess low-N stress tolerance for various levels of N deficiency. Studies carried out by CIMMYT have shown that genotypes selected for drought tolerance also perform well under low-N conditions. This indicates that CIMMYT's selection for drought tolerance at flowering can simultaneously improve tolerance to low-N stress (Edmeades et al., 1995). Secondary traits, such as improved N uptake, high plant nitrate content, increased nitrate reductase activity (Feil et al., 1993), extensive translocation from the stover to grain (Eghball and Maranville, 1991), a large leaf area, and high specific leaf N content (Muchow and Davis, 1988), have been found to be positively correlated with yield under N-limited situations.

Grain nitrogen concentration

The concentration of protein in maize grain has received relatively little attention by breeders. The importance of the genetic constitution for the concentration of protein in maize grains has been demonstrated by the selection experiment, which started in 1896 at the Illinois Agricultural Station. After 90 generations of selection for high and low levels of grain protein, the grain protein was modified from 10.9% in the original cultivar, Burr's White dent corn, to 4 and 32%, respectively. The protein level of the low-protein strain seems to have reached a plateau, but progress in selecting for high protein is thought to be possible (Dudley and Lambert, 1992). Many other researchers reported genotypic variation in grain N concentration (Feil, 1998; Feil et al., 1990).

Nitrogen use efficiency

Uptake and translocation of N in maize are under polygenic control (Pollmer et al., 1979). Muruli and Paulsen (1981) found genotypic variation in NUE, thus enabling breeders to improve this trait. In contrast to the strategies for breeding for drought-tolerant genotypes, it is unclear whether breeding for improved NUE should be done at a low, moderate, or high level of N fertility. Expression of genetic variability in NUE depends largely on the level of N fertilization. Various investigators have shown that the maize grain yield can be affected by the interactions between

the genotype and the level of N fertilization (Landbeck, 1995; Moll et al., 1987). Higher-yielding hybrids are usually expected to exhibit a higher average NUE. However, if hybrid by N level interactions occur, the ranking of hybrids may differ for NUE versus mean yield. This is the case when, for example, of two hybrids with the same mean grain yield averaged over a range of N levels, the hybrid that yields more at lower N levels would have a higher average NUE (Moll et al., 1987). Muruli and Paulsen (1981) found that NUE can be improved by selection, but at the cost of lower grain yields under high levels of soil N. In the study of Presterl et al. (2002), the grain yields of two European hybrids did not differ significantly at high N supply. Hybrids developed under low N, however, out-yielded hybrids developed under high N by 11.5% under low N, and by 5.4% at medium N supply, respectively. The 'low-N' hybrids took up significantly more N under low (12%) and medium (6%) N supply than the 'high-N' hybrids. On the other hand, they did not find any differences in the N_utE of hybrid types, developed at low or high N. Different findings showed close correlations of either N_utE or N uptake efficiency with the grain yield under low N. These correlations varied among sites and/or genotypes (Kling et al., 1996; Lafitte and Edmeades, 1994; Sallah et al., 1996). Breeding for grain yield seems to change the contribution of post-floral N uptake to total N uptake. Tollenaar and Wu (1999) compared older and newer short-season Canadian hybrids and found that the proportion of N in the grain that derived from post-silking N uptake was 60% for the newer hybrids and 40% for the older ones. The same observation was made by Muruli and Paulsen (1981). Availability of soil N at a particular development stage must, therefore, be taken into account when comparing genotypes. This is especially true when experiments are conducted under low-N conditions, when mineralization contributes considerably to the N supply.

Moll et al. (1987) found that NUE, averaged over N fertilizer rates, was an effective selection criterion for enhancing the responsiveness to N fertilization. According to Lafitte et al. (1997), a reasonable strategy for breeding productive maize under N-limited conditions would be to develop early- and late-maturing source populations, which take up large quantities of N, partition a large proportion of plant N to the reproductive structures (high NHI), and maintain a high N concentration in grain under limited N supply. Lafitte et al. (1997) found that the HIs for biomass and N of landraces were less affected by a soil N deficiency and that the advantage of secondary traits in the selection for low-N tolerance was less evident than for drought tolerance. This is reflected in the weighting of traits that are genetically variable and enable the assessment of tolerance to drought or low-N in current stress breeding programmes of CIMMYT. In the low-N breeding programme, the trait grain yield is weighted at 50%, ears per plant and leaf senescence

at 20% each, and ASI at 10%. In the drought tolerance breeding programme, grain yield is weighted at 33%, ears per plant at 20%, leaf senescence, tassel size, and ASI at 13% each, and leaf rolling at 7% (Banziger et al., 2000).

2.4.3. Maize Breeding in Thailand

In Thailand, the temperature is high and rainfall unpredictable at the beginning of the growing season. Thus, a water deficit is likely to occur at the pre-anthesis stage of maize (Kitbamroong and Chantachume, 1992). Therefore, a national maize breeding programme for early drought tolerance was established already in 1982. In this programme, drought stress was applied from 35 to 55 days after planting. A promising drought-tolerant population (KK-DR) and some OPVs resulted from this selection programme, which was conducted at the Nakhon Sawan Field Crops Research Centre (Manupccapan et al., 1997). In the central and northern regions of Thailand, downy mildew (*Peronosclerospora sorghi*) is a major biotic stress, against which improved OPVs and hybrids show a good level of genetic resistance (Dowswell et al., 1996). This material must be improved further in terms of tolerance to drought and low-N (Leon and Paroda, 1993). The private seed industry in Thailand considers drought-tolerance to be a main goal in the breeding of inbred lines and hybrids (Vichien Sakulsom, UNISEEDS CO, LTD., personal communication). At present, CIMMYT is carrying out a research project entitled 'Developing New Maize Germplasm Through Biotechnology for Resource-Poor Farmers in Asia' with the objective of strengthening the capacity of the national agricultural research system in the use of biotechnology tools. The aim is to develop maize germplasm that is resistant to major diseases and tolerant to drought and low-N by means of molecular marker-assisted selection (Asian Development Bank, 2001).

2.5. Grain Minerals

The widespread incidence of so-called "Hidden Hunger", i.e. malnutrition due to mineral and vitamin deficiency (Welch and Graham, 2004), throughout the world has raised the level of interest of nutritionists and agronomists in the minor constituents of food (Peters et al., 2003). High levels of minerals and protein are usually considered to be indicators of a high dietary quality of cereal products for humans and farm animals. However, this may not be true at least for P. Approximately 80% of the P in maize grains occurs as phytic acid (Lott et al., 2000). With

utilization rates of 40% and below, maize phytic acid is a relatively poor source of P for pigs, poultry, and other monogastrics (Lantzsch et al., 1991). Phosphorus from undigested phytic acid may contribute to the eutrophication of surface waters in areas in which large amounts of animal waste are applied. Furthermore, phytic acid is thought to act as a naturally occurring toxic substance (Feil, 2001). Crops obtain their mineral nutrients from the soil. There is concern that growing cereal varieties, bred for high levels of grain minerals, will lead to a depletion of soil nutrient reserves and will, thus, be unsustainable without the addition of fertilizer (Feil et al., 1992a; Graham et al., 1999). One way to avoid this dilemma would be to increase the bioavailability of grain minerals rather than to increase their concentration (Van Campen and Glahn, 1999).

Increasing the grain protein concentration has, thus far, not been a major goal of most maize breeding programmes, because the nutritional value of ordinary maize protein is low for non-ruminants due to its low concentrations of the essential amino acids lysine, tryptophan, and methionine (Olsen et al., 2003; Pixley and Bjarnason, 2002). It is well established that the concentrations of N (Bletsos and Goulas, 1999; Dudley and Lambert, 1992; Kniep and Mason, 1991) and minerals (Ahmadi et al., 1993; Arnold and Bauman, 1976; Arnold et al., 1977; Raboy et al., 1989) can vary among varieties. Research conducted in the lowlands of Thailand revealed that the grains of tropical maize varieties differ markedly in the concentrations of N, P, and, to a lesser extent, K (Feil et al., 1992a; Feil et al., 1993). Little has been published about the genotypic variation in the concentrations of mineral elements other than P and K in the grain of tropical maize. Banziger and Long (2000) grew more than 1400 improved maize genotypes and 400 landraces in 13 trials in Mexico and Zimbabwe and found genotype differences in the concentrations of grain Fe and Zn. Maziya-Dixon et al. (2000) observed large variation in the concentrations of grain Fe and Zn in a set of 109 inbred lines that were developed for the mid-altitude and lowland agroecologies of West and Central Africa.

Since N is the most limiting factor for plant growth on many soils, the application of N fertilizer usually results in marked increases in grain yield. It is suggested that large increments in grain yield, due to N fertilization, tend to dilute the grain minerals. Nevertheless, N fertilization had little or no effect on the concentrations of P and K in maize grains in most studies (Ahmadi et al., 1993; Alfoldi et al., 1994; Bennett et al., 1953; Feil et al., 1993; Thiraporn et al., 1992).

Surprisingly few studies dealt with the effect of water supply on the concentration of minerals in the grain. Harder et al. (1982) imposed various moisture stress treatments on maize after silking. Even though this resulted in grain yield reductions of up to 33%, no changes in the concentrations

of grain P and K were observed. Although it is assumed that 50% of the losses in maize grain yield in the developing world result from pre-anthesis drought stress (Edmeades and Deutsch, 1994), no information seems to have been published about the effects of this pre-anthesis drought on the mineral composition of maize grains.

Nitrogen and minerals are distributed unevenly throughout the maize kernels. The highest concentrations of minerals are found in the germ, whereas the endosperm is almost void of mineral elements (O'Dell et al., 1972). Varietal differences in the concentration of grain N and minerals may, therefore, be due to variation in the relative size of the major kernel components. One of the objectives of this study was to determine whether the grain of tropical maize varieties differ in the concentrations of minerals other than P and K (Mg, Ca, Mn, Zn, and Cu) and to which extent varietal differences are modified by the interactive effects of N fertilization and water regime. The grains of two of the four tested varieties which differed in the concentration of N and several mineral elements in the grain were dissected to determine whether the variation in grain N and P concentration can be attributed to variation in the size of germ and endosperm.

2.6. Objectives

In developing countries, it is estimated that about 30% of the average gap between potential and actual grain yields in farmers maize fields are due to drought and N deficiency, with both stresses often occurring simultaneously. While the single effects of irrigation and N application on the grain yield, grain yield components, and N-related parameters of maize have been reported in numerous publications, relatively little has been published about the interactive effects of these factors, especially for tropical maize.

As a rule, research has focussed on the response of maize to water shortage around silking or later, whereas the effects of water deficit before tasseling have received relatively little attention. However, the probability of drought is highest at the beginning of the growth season in many maize production areas. Knowledge of the effects of pre-anthesis drought on grain yield and yield components is primarily related to temperate maize.

The main objective of this study was, therefore, to determine the interactive effects of pre-anthesis water availability, N fertilizer rate, and variety on the grain yield, yield components, HI, N accumulation, NUtE, and AFNR of maize in the tropical lowlands of Thailand.

Another objective of the research was to determine whether tropical maize varieties differ in the

concentration of grain protein and grain minerals other than P and K (Mg, Ca, Mn, Zn, Cu) and to which extent varietal differences are modified by the interactive effects of N fertilization and water regime. Furthermore, grains were dissected to determine whether the variation in grain N and P concentration can be attributed to variation in the size of the germ and endosperm.

The worldwide approaches to improving the stress tolerance of maize varieties have a high potential to increase and stabilize the yields in fields of resource-poor farmers. The results of this study are expected to provide information about the interactive effects of drought and N deficiency on the grain yield and quality of maize for breeders engaged in programmes for tolerance to drought stress and low soil fertility of tropical maize.

3. MATERIALS AND METHODS

3.1. Plant Material

Two open-pollinating varieties, Suwan 1 and La Posta Sequia, and two hybrids, KTX2602 and DK888, were used. Suwan 1 (C11) is a yellow semi-flint type, derived from Caribbean, Mexican, and Philippine populations. It was released in Thailand in 1975 and has been used since then as a source of germplasm for resistance to downy mildew in many tropical maize breeding programmes worldwide. It is still the traditional check variety for Thai Breeders. La Posta Sequia (C4), a late maturing, lowland white dent population, originates from a drought tolerance selection programme of CIMMYT, which began in the 1970s. CIMMYT applied drought stress at different levels of intensity during flowering and grain filling and selected for several traits associated with drought tolerance using an S_1 recurrent selection scheme (Bolaños and Edmeades, 1993a; Byrne et al., 1995). La Posta Sequia showed yield improvements under severe N deficiency, too (Banziger et al., 1999). The Thai three-way hybrid, KTX2602 (also known as Suwan 2602 and KUH2602), was bred by the Kasetsart University and officially released in 1986; it has a close genetic relationship to Suwan 1. The single-cross hybrid DeKalb888 (DK888), a semi-prolific type, was released in 1991 and was the most successful variety in Thailand in the 1990s.

3.2. Soil Properties and Nitrogen

The soil is an ustic, isohyperthermic, kaolinitic oxisol (Camp, 1996). Table 1 gives the properties of the experimental field. The data are based on eight randomly collected, bulked samples. The soil texture and organic matter were analysed by the Central Laboratory of the Kasetsart University, Thailand in 1995 (Soil Science Department, 1994). The bulk densities were measured by Camp (1996). The other parameters were determined in the laboratories of Lonza AG, Basle, Switzerland in 1992. The nutrients were extracted with ammonium acetate-EDTA (0.5 M NH_4Ac + 0.5 M HAc + 0.02 M EDTA; pH 4.65); the soil/solution ratio was 1:10 and the extraction time 30 min. According to the report of Lonza AG, the cation exchange capacity was low in both soil layers. In the topsoil, the availability of P, K, Zn, Mn, Fe, and B was low, that of Mg and Ca

moderate, and that of S, Cu, and Mo sufficient. In the subsoil, the availability of P, K, Ca, Zn, Mn, Fe, B, and Mo was low, that of Mg moderate, and that of S and Cu sufficient. The concentration of Al in the subsoil was relatively high, and the concentration of Co was considered to be toxic to plants. Despite the high clay content, the cation exchange capacity was low.

Table 1: Properties of two soil layers (5 to 30 cm and 30 to 60 cm) of the experimental field.

<u>Parameter</u>	<u>Unit</u>	<u>5 - 30 cm</u>	<u>30 - 60 cm</u>
clay ^{a)}	g kg ⁻¹	550	740
silt ^{a)}	g kg ⁻¹	220	130
sand ^{a)}	g kg ⁻¹	230	130
pH (H ₂ O/acetate)		6.6/6.9	5.1/6.6
organic matter ^{a)}	g kg ⁻¹	21	13
bulk density ^{c)}	Mg m ⁻³	1.23	1.17
P ^{b)}	mg kg ⁻¹	8	8
K ^{b)}	mg kg ⁻¹	35	23
Mg ^{b)}	mg kg ⁻¹	126	198
Ca ^{b)}	mg kg ⁻¹	1537	970
S ^{b)}	mg kg ⁻¹	76	30
Zn ^{b)}	mg kg ⁻¹	0.2	0.2
Mn ^{b)}	mg kg ⁻¹	19	4
Cu ^{b)}	mg kg ⁻¹	1.9	1.4
Fe ^{b)}	mg kg ⁻¹	16	11
B ^{b)}	mg kg ⁻¹	0.17	0.09
Mo ^{b)}	mg kg ⁻¹	0.34	0.15
cation exchange capacity ^{b)}	meq kg ⁻¹	163	144
salinity (KCL) ^{b)}	mg kg ⁻¹	150	153

^{a)} Central Laboratory of Kasetsart University, Thailand in 1995

^{b)} Ammonium acetate-EDTA, at pH 4.65; Lonza AG, Basle, Switzerland in 1992.

^{c)} Camp, 1996

The higher pH of the topsoil was probably due to irrigation with ground water rich in calcium carbonate (Ca 102 mg kg⁻¹), which comes from the surrounding limestone hills (Neidhart, 1994). The water permeability of the soil was moderately high. The fraction of plant-available water was small (12 to 15%, in soil matrix potential between -5 and -1400 kPa) (Camp, 1996).

Contents of mineral N in the soil (N_{\min} ; includes only nitrate, $\text{NO}_3\text{-N}$) were measured just before planting, during vegetative growth, and at physiological maturity. Nine samples, from each of three replications, were taken in the plant rows at depths of 5 to 30 cm and 30 to 60 cm. One hundred grams of soil (fresh weight) were dissolved in 120 mL 0.01 N CaCl_2 solution and shaken for 90 min.. The nitrate concentration was determined reflectometrically (Reflectoquant[®], Merck). The initial N_{\min} values of the three experimental years were averaged because the sampling dates and the concentrations of nitrate varied strongly over the years. Apparent N mineralization (ANM) is total shoot N plus root N plus residual N_{\min} in the soil at maturity minus soil N (fertilizer N plus N_{\min} at planting). This trait serves to examine differences in the delivery of mineralized N due to drought stress and N fertilization. It balances N losses from leaching, volatilization, and immobilization with N input from fertilization, mineralization, and the atmosphere (Banziger, 1992; Elbehri et al., 1993).

3.3. Agricultural Practices

All three main experiments were conducted at the same experimental site in the dry seasons of 1995, 1996, and 1997. The whole field was previously planted with maize, without fertilizer, in order to deplete the soil of N. The mature plants were removed at the end of the rainy season. Maize stubbles and weed were left as mulch and were incorporated into the soil with a harrow. The degree of N depletion depended on the soil moisture, the date of clearing and harrowing, and the amplitude of the subsequent rainfalls, which promoted nitrate leaching at the end of the rainy season.

Shortly before sowing, the field was ploughed with a disc harrow to refine the seed bed. Ridges at intervals of 0.75 m, 20 cm higher than the furrows, were formed with a cultivator before fertilizer application and planting of maize. At the end of each experimental main block, a dike was built to stop the flow of water in the furrows, with the aim of even distribution of water in the corresponding irrigation unit.

Fertilizer was applied manually on the top of the ridges. Before planting the maize, 50 kg triple super-phosphate with 46% P_2O_5 and 50 kg muriate of potash with 60% K_2O were applied to all the plots; 80 kg sulfate of ammonia (NH_4) SO_4 with 21% N (and 24% sulfur) were added to the N80 and N160 treatments and incorporated afterwards. At approximately 30 days after emergence (DaE), an additional 80 kg N fertilizer were side-dressed along the ridges of the N160 treatment

and irrigated into the soil.

Planting was done on 22nd December 1994, 13th December 1995, and 18th December 1996. Two seeds per hill were sown manually at intervals of 0.25 cm. Approximately two weeks after emergence, the less vigorous plant per hill was removed to ensure a homogenous stand with a target plant density of 5.3 plants m⁻².

Pre-emergence chemical weed control was accomplished with a mixture: Atrazin® (4 kg ha⁻¹) and Stomp® (4.7 l ha⁻¹). Itchgrass (*Rottboellia exaltata* L.) and purple nutsedge (*Cyperus rotundus* L.) were not effectively controlled by these herbicides, thus, weeding was done additionally by hand. Dressing with Gaucho® protected the seeds and young plants from attack by insects. An application of Monocrotophos (750 ml ha⁻¹ as 60% solution) to ward off frit fly (*Oscinella frit*) was indicated in the first year only.

3.4. Irrigation

On Farm Suwan, water can be applied to the fields by sprinkler or by furrow irrigation. Sprinklers are preferable, because they are easy to handle, especially at planting and at early stages of plant development. During the dry season, however, strong winds often lead to an unequal water distribution. Furrow irrigation applies water more homogeneously, especially on small areas. The ridges must be tilled perfectly, the furrows must be free of soil clods and harvest residues, and they must have an even slope to guarantee a homogenous distribution of water. A slope of 0.4% usually enables the water to reach the end of a field 100 m long. However, under sub-optimum conditions, i.e., when the soil is very dry or the furrows are uneven, the irrigation treatment might take too long, resulting in an unequal distribution of water and nitrate in the soil (N losses by leaching) at the beginning and the end of the furrows. Thus, the furrows in the experiments were at most 50 m long.

Throughout the growing season, the control treatment (referred to as *well-watered regime*) was irrigated weekly by sprinkler or furrow irrigation at a rate that corresponded to the estimated ET of approximately 30 to 40 mm. After sowing, sprinkler irrigation was applied three (1995 and 1997) or four (1996) times to all the plots every four to five days to ensure the establishment of the plants. Thereafter, the first drought stress period started. It occurred in the following development stages (described as 'V' stages, e.g., V2 = two leaves with visible leaf collars) of the *drought-stressed* maize plants with 80 kg N ha⁻¹ (the number of days with effective stress are

indicated in brackets): in 1995 from V2 to V6 (20 days), in 1996 from V3 to V6 (16 days), and in 1997 from V2 to V6 (22 days). Thirty-two DaE, a single sprinkler irrigation was applied to the whole field. Thereafter, the second stress period was initiated. It lasted from V7 to V11 (17 days) in 1995, from V8 to V14 (20 days) in 1996, and from V7 to V10 (14 days) in 1997. Irrigation was resumed right before the earliest cultivar (KTX2602) started to flower. Thereafter, weekly furrow irrigation ensured a sufficient water supply to all the plants until the harvest.

This water regime was applied in order to considerably stress the maize plants during the vegetative phase including some phases of the reproductive development. The development of the reproductive organs of maize begins approximately three weeks after germination with the initiation of the tassel and the axillary meristem (potential ears) (Motto and Moll, 1983). At the same time, the stalk initiates a period of greatly increased elongation (Hanway and Ritchie, 1971). During these phases, the effect of the first stress period was assumed to be at maximum. According to Tollenaar and Dwyer (1999), the transition of the axillary meristem to ears (about 10 days after tassel initiation) is affected by environmental conditions of the following weeks, which limits the final number of ears usually to one or two, and under unfavourable conditions, to none.

After interrupting the drought stress through irrigation, the beginning of the second stress phase was supposed to affect the establishment of the final ears. All the leaves are initiated by the time the plant reaches the V8 to V10 stage (Tollenaar and Dwyer, 1999). At about V10, the well-watered maize plants begin to show a rapid, steady increase in dry weight and nutrient uptake. Two leaf stages later, the number of ovules (potential kernels) on each ear and the size of the ear are determined. In the experiments, the stress periods were terminated after the number of kernel rows per ear was assumed to be established. The determination of the number of kernels per row, however, is not complete until about one week after silking (Hanway and Ritchie, 1971), i.e. after the irrigation had been resumed.

3.5. Meteorological Data

Data on temperature, humidity, evaporation, and rainfall were systematically recorded at a meteorological station on Farm Suwan.

3.5.1. Growing Degree Days

Growing Degree Days (GDD) were calculated as described by Nielson and Hinkle (1996), using the 10 to 32 heat stress method (Table A1). The base temperature (T_{\min}) was 10°C. The daily maximum temperature (T_{\max}) was reduced by the number of degrees, by which the maximum temperature exceeded 32°C. GDD were then calculated as (1):

$$GGD = \frac{T_{\max} - T_{\min} - 10}{2} \text{ } ^\circ\text{C} \quad (1)$$

3.5.2. Evapotranspiration

In arid regions, 90% of the precipitation returns to the atmosphere through evaporation and ET (Rosenberg et al., 1983). Evapotranspiration (ET) combines evaporation from soil and the plant surface, and transpiration through the plant surface, whereby water is transformed to water vapour. To describe the actual ET, factors such as soil parameters, soil water content, soil fertility, the specified crop at a designated time or growth stage, and other agricultural factors must be considered. The effect of crop characteristics (duration of developmental stages) and time (growing season) on the water requirements of the crop is given by the crop coefficient (K_c) (Burman and Pochop, 1994). According to Doorenbos and Pruitt (1977), K_c of the maize crop ranges from 0.2 to 1.2. In this experiment, the actual ET is defined as Evapotranspiration crop (ET_{crop}). ET_{crop} can be found by (2):

$$ET_{\text{crop}} = K_c \times ET \quad (2)$$

Annual variations in the weather conditions may affect the seasonal ET; in the dry season, ET is influenced mainly by temperature and wind (Howell et al., 1998). K_c depends on the length of the development stages, which, in turn, are dependent on temperature (Howell et al., 1998). However, Nielson and Hinkle (1996) found that, during the period prior to full soil cover, time-based K_c produced more accurate estimates of maize ET. Because drought stress in this study was applied before flowering, ET was, therefore, calculated based on time (Table A1). In line with Doorenbos and Pruitt (1977), K_c was adapted to the different growing patterns during the three experimental years; and seasonal differences were taken into account by adjusting the year-specific duration of the following four crop growth stages: initial, crop development, mid-season, late season, and harvest, as shown in Table 2.

Table 2: Length of growth stages, and corresponding K_c values in 1995, 1996, and 1997 (Doorenbos and Pruitt, 1977)

<u>Growth stages</u>	K_c	Days after planting		
		<u>1995</u>	<u>1996</u>	<u>1997</u>
Initial	0.53	25	25	25
Crop development	0.75	30	35	30
Mid-season	1.05	45	45	40
Late season	0.55	30	30	25
Harvest	0.3	12	12	4

3.5.3. Pan Method

Data from the meteorological station (500 m away) were not accurate enough to calculate the ET by the modified Penman method (Burman and Pochop, 1994), which provides the most accurate results of all the methods described by Doorenbos and Pruitt (1977). The Pan method, given a proper positioning, gives the ET at weekly or longer intervals with possible errors of 15%. Pan evaporation (E_{pan}) is the evaporation of water from a container in an environment, in which water evaporates readily. Daily measurements record the loss of water in mm/day. The E_{pan} reflects the integrated effects of radiation, wind, temperature, and humidity on the evaporation from a specific surface of water. Differences in the reflection of solar radiation and in diurnal variations in the transpiration of the crops require empirically derived pan coefficients (K_p) that take into account the climate and the environment of the pan. The pan used was a US class A pan type (121 cm in diameter) surrounded by a dry, bare area at a distance of at least 100 m from the next planted and irrigated field. The wind was usually light to moderate, and the mean relative humidity ranged from 40 to 70%. Based on the experimental studies described by Doorenbos and Pruitt (1977), the wind and humidity measurements gave a K_p of 0.6.

3.6. Plant Parameters

Apart from the presented results, other parameters were surveyed and used to interpret the results. Thus, the sampling of these parameters is described below, too.

3.6.1. Sampling Before Flowering

Shoot dry matter accumulation

From around 20 DaE until 70 DaE, six to twelve whole plants per plot were harvested at weekly intervals for the determination of above-ground shoot fresh (FM) and dry matter (DM). Samples were cut by hand or by a shredder; after drying in the sun, they were dried in an oven at 70°C to constant weight.

Morphological Parameters

The number of green and dead leaves of 12 marked plants were counted weekly. Senescence is defined as the percentage of dead leaves from the total number of leaves. The leaf rolling index (LRI) was estimated visually twice a week during the two most intense periods of stress. A leaf rolling score of '1' indicates that the leaves are unrolled; at the other end of the scale, an LRI of '5' indicates tightly rolled leaves. Plant and ear height were measured shortly after anthesis and at the black layer stage. Plant height is the distance from the surface of the soil to the collar (*ligula*) of the last developed leaf; ear height is measured from the surface of the soil to the node of the uppermost ear.

Plant Analysis

Shoot samples were taken four times until anthesis, dried as described above, ground, and assayed for concentrations of total N, P, and K. Samples were digested in sulfuric acid (5 ml of H₂SO₄ : Na₂SO₄ : Sc = 1000 : 100 : 1) at 360 to 400°C. Nitrogen and P were determined with an Auto Analyser (Technicon[®] Auto Analyzer II); K was determined by atomic absorption spectrophotometry (Soil Science Department, 1994).

3.6.2. Sampling at Flowering

Anthesis-Silking Interval

Days to anthesis and days to silking were recorded daily for each sub-subplot. 'Silking' refers to the stage at which silk emerged on 50% of the observed plants. 'Anthesis' was reached when 50% of the plants shed pollen from the main branch of the tassel and from few other branches. The anthesis-silking interval (ASI) is the number of days from anthesis to silking; a positive ASI indicates that anthesis occurred before silking.

3.6.3. Sampling at Physiological Maturity

Black Layer Maturity

Two ears per plot were examined for physiological maturity from 90 DaE onwards. A sample of 10 kernels per ear was removed from the middle of an ear, cut lengthwise along the germinal-abgerminal plane, and the development of the black layer was investigated. Black layer maturity was considered to be reached when 60% of the kernels had a distinct black layer (Carter and Ponoleit, 1973).

Biomass

At physiological maturity, 3.77 m² (1995) and 5.66 m² (1996, 1997) were hand-harvested from the inner rows of each sub-subplot to determine total stover DM, grain yield, and yield components, as well as the contents of N and minerals in the grain and stover. Grain and stover samples were dried at 70°C to constant weight. Stover DM consists of all the leaves, the stem, the cob, and the husks.

Twelve randomly selected plants and ears were used to determine the number of ears per plant, kernel rows per ear, and kernels per row. The 1000-kernel weight (TKW) was calculated from the weight of 200 dry kernels from each plot. The number of kernels (kernel number) per area was calculated by dividing the grain yield m² by the single kernel weight. The number of kernels per row was calculated by dividing the kernel number m² by the number of ears m² and the kernel row number per ear. The harvest index (HI) is the ratio of grain yield to total above-ground biomass.

3.6.4. Nitrogen-Related Parameters

Plant Nitrogen

The apparent recovery of mineral fertilizer N (AFNR) is the difference in the total shoot N of fertilized and unfertilized plots, expressed as a percentage of the rate of N application (Van Dijk and Brouwer, 1998). The N harvest index (NHI) is the ratio of grain N yield to total above-ground shoot N. This parameter is indicative of the partitioning of N to the grain. The reciprocal value of the shoot DM to shoot N ratio is the shoot N concentration (SNC). The N use efficiency (NUE) is the grain yield per unit available N in the soil and is expressed as g grain DM g⁻¹ soil N (Moll et al., 1982). Nitrogen use efficiency can be broken down into N uptake efficiency and

N utilization efficiency (Muchow, 1988b). Nitrogen uptake efficiency is the amount of total plant N per unit soil N and describes the efficiency of N absorption in g total N g^{-1} soil N. Nitrogen utilization efficiency (NUE) is the efficiency, with which absorbed N is utilized by the plant to produce grain and, thus, is g grain DM g^{-1} total shoot N.

The high biomass production and the amounts of residual N_{min} (see 3.2.) in non-fertilized plots after maturity led to the conclusion that a considerable amount of N was provided to the plants through N mineralization throughout the growing season. Therefore, NUE was refined to NUE_{min} by taking into account apparent N mineralisation (definition see 'Soil N') during the growth period, while NUE_{fert} includes only the initial nitrate in the soil plus fertilizer N. The mineralization of N is calculated as follows: total plant N plus estimated N content in the roots (5% of total N) plus remaining N_{min} at maturity minus initial N_{min} . Total soil N contents are means of total N_{min} in treatments without N fertilization under drought-stressed or well-watered conditions in each experimental year.

3.6.5. Minerals in the Grains

Whole Kernel Analyses

Aliquots of the grains (400 g) were dried at 70°C to constant weight to determine grain yield. Sub-samples of about 50 g were ground with a Cyclotec Tecator 1093 mill (Tecator, AB, Höganäs, Sweden) and passed through a 1-mm screen. Analyses of the concentration of total N were performed with a LECO CHN-1000 auto analyzer (LECO cooperation, St. Joseph, MI, USA). To determine the concentrations of P, K, Mg, Ca, Mn, Zn, and Cu, duplicate 1 g samples were ashed in silica crucibles at 550°C for 7 h in a muffle furnace. The residue was taken up in 8 ml of 6.8 M HCl, transferred to a 50-ml volumetric flask, and, after adding 1 ml 0.38 M CsCl solution, diluted to the mark with deionized water. After passing the solution through a membrane filter (Merck 3558011, E. Merck AG, Darmstadt, Germany), an aliquot was analyzed with an Inductively Coupled Plasma Atomic Emission Spectrometer, (ICP-AES, Liberty 200, Varian Australia Pty. Ltd., Mulgrave, Victoria, Australia) to determine the mineral element concentrations.

Concentrations of Nitrogen and Phosphorus in Germ and Endosperm

In 1995 and 1996, about 40 kernels from each plot were soaked in distilled water for about 24 hours. Thereafter, the pericarp was peeled off and discarded. The germ was separated from the

endosperm by exerting slight pressure on the kernel. Endosperm material that adhered to the germ was removed with a sharp knife. The germ and endosperm samples were dried, ground, sieved, and assayed for total N as described above. The concentration of P was determined according to a modified version (Feil and Fossati, 1997) of a procedure described by Jones and Case (1990). Five hundred milligrams of ground material were weighed into a digestion tube, and 3 mL of concentrated HNO₃ were added. The samples were left overnight at room temperature. After adding 1 mL conc. H₂SO₄, the tubes were placed in the port of a digestion block and first heated to 150°C for 30 min, then to 175°C for 60 min, and finally to 230°C for 90 min. The clear digest was neutralized with NaOH and *p*-nitrophenol as an indicator (Olsen and Sommers, 1982), and P was determined colorimetrically according to Murphy and Riley (1962).

3.7. Statistical Analysis

3.7.1. Layout of the Experiments

The design was a split-split-plot design with six replications. Each replication was divided into two main plots, which differed in water supply (well-watered and drought-stressed). The three N levels 0, 80, and 160 kg N ha⁻¹ were the sub-plots (N0, N80, and N160); they were laid out in strips to avoid lateral seepage of the N fertilizer. The four varieties (Suwan 1, La Posta Sequia, KTX2602, and DK888) were the sub-sub-plots. The development of vegetative biomass, which was observed during the first two years, required relatively large plots (54 m², 9 m long and 6 m wide). In the last year, the plot size was 12.2 m², 3.25 m long and 3.75 m wide. The row spacing was 0.75 m.

3.7.2. Statistical Methods

All the statistical analyses were carried out using the SAS[®] (Statistical Analysis System) programme (SAS Institute Inc., 1997). The SAS calculation method for mixed linear models, PROC MIXED, is based on the estimation maximum likelihood or restricted maximum likelihood of linear statistical models involving both fixed and random terms, such as the linear model underlying the split-plot analysis (Littell et al., 1996), and was, thus, perfectly suited for this study. PROC MIXED ensures a correct analysis of split-split-plot experiments including comparisons and mean separation tests. In PROC MIXED, the replication by water and the replication by water by N effects are part of the random statement, indicating that they are random

rather than fixed effects. Plant density was used as a covariate to reduce the experimental error and to adjust the treatment means of water regime and N fertilization for the interpretation of the varietal results. Separation of the means was performed only when the *F*-test indicated significant ($P < 0.05$) differences among the treatments (Fisher's protected LSD test).

4. RESULTS

4.1. Grain Yield, Yield Components and Harvest Index

4.1.1 Effect of Water Regime and N Rate on Grain Yield

The 1996 season yielded most with 6.59 Mg ha^{-1} , while the yields were similar for the years 1995 and 1997 with 5.42 Mg ha^{-1} and 5.70 Mg ha^{-1} respectively. Drought stress and low N supply reduced grain yield in all the years. At N0, where plants relied only on mineralized soil-N, the average grain yield of the four varieties was about 5.00 Mg ha^{-1} . In all years, N fertilizer application significantly increased grain yield, but the N effect depended on the availability of water. In general, plants profited more from a higher N rate under well-watered conditions than under drought stress, where an additional 80 kg ha^{-1} N in the N160 treatment did not increase grain yield anymore (Figure 1).

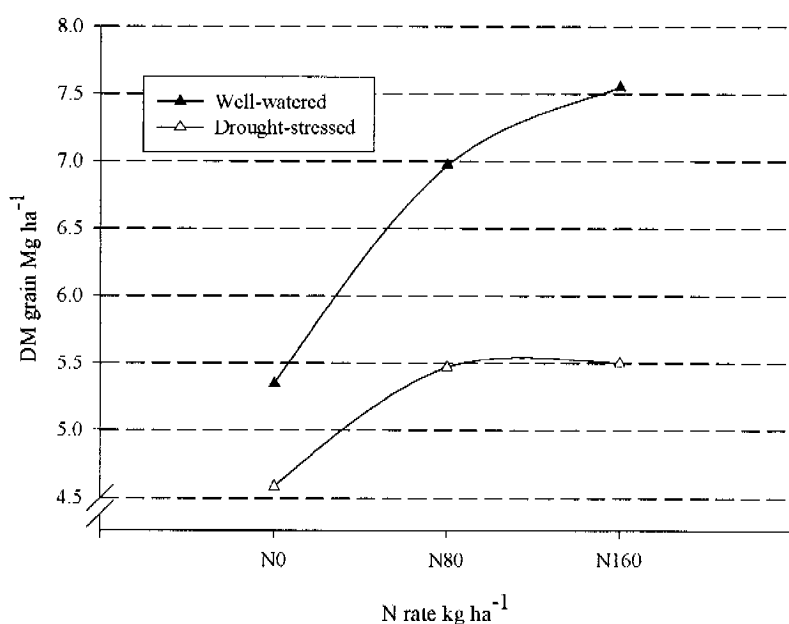


Figure 1. Effect of N level on grain yield under well-watered and drought stress conditions; average of four varieties and three years.

Reductions in grain yield due to drought and N deficiency were not consistent over the various years, which required a breakdown according to years (chapter 3.7. Statistical Analysis). When statistically ($P=0.05$) significant interactions occurred in at least two of the three experimental years, then the data from the third year are also presented to show whether there are similar trends.

Averaged across the N rates and varieties, the grain yields of drought-stressed maize were lower by 32% (1995), 13% (1996), and 21% (1997) than that of well-watered maize; the water effects were significant at $P \leq 0.05$ (Table 4). The water by N rate interaction was statistically significant in 1995 and 1997, while the water regime by variety interaction was significant in 1996 and 1997 (Table 4). The data for these interactions are shown in the Tables 3, 10, and 11.

Table 3: Effects of the water regime x rate of N application interaction on grain yield, total shoot dry matter, and kernel number in 1995, 1996, and 1997.

	Grain yield (Mg ha ⁻¹)			Total shoot dry matter (Mg ha ⁻¹)			Kernel number m ⁻²		
	1995	1996	1997	1995	1996	1997	1995	1996	1997
WW [†] x 0 kg N	4.68	6.51	4.84	10.9	13.5	12.2	1710	2240	1910
DS x 0 kg N	3.86	5.81	4.08	7.2	11.2	9.0	1520	2050	1670
<i>F</i> -test	*	*	*	***	**	***	ns	ns	*
WW x 80 kg N	6.97	7.10	6.83	16.0	15.0	16.8	2340	2360	2530
DS x 80 kg N	4.64	6.32	5.44	8.6	12.2	11.8	1710	2150	2070
<i>F</i> -test	***	*	***	***	***	***	***	*	***
WW x 160 kg N	7.73	7.47	7.45	17.4	15.6	18.8	2510	2430	2670
DS x 160 kg N	4.62	6.33	5.55	8.5	12.2	12.2	1670	2150	2100
<i>F</i> -test	***	**	***	***	***	***	***	*	***

*, **, *** significant at $P=0.05, 0.01, 0.001$, respectively. ns not significant.

[†] WW well-watered, DS drought-stressed.

Table 4: Main effects of water regime, rate of N application, and variety on grain yield, total above-ground dry matter, and harvest index in 1995, 1996, and 1997; results of the *F*-tests for the effects of main factors and interactions

	Grain yield (Mg ha ⁻¹)			Total shoot dry matter (Mg ha ⁻¹)			Harvest index		
	1995	1996	1997	1995	1996	1997	1995	1996	1997
Grand mean	5.42	6.59	5.70	11.5	13.3	13.5	0.49	0.50	0.43
<u>Water regime</u>									
Well-watered	6.46 a [†]	7.03 a	6.37 a	14.8 a	14.7 a	15.9 a	0.44 b	0.48 b	0.40 b
Drought-stressed	4.37 b	6.15 b	5.02 b	8.1 b	11.9 b	11.0 b	0.54 a	0.52 a	0.46 a
<u>N rate</u>									
0 kg N ha ⁻¹	4.27 b	6.16 b	4.46 c	9.0 b	12.4 b	10.6 c	0.49	0.50	0.42
80 kg N ha ⁻¹	5.81 a	6.71 a	6.14 b	12.3 a	13.6 a	14.3 b	0.49	0.49	0.43
160 kg N ha ⁻¹	6.18 a	6.90 a	6.50 a	12.9 a	13.9 a	15.5 a	0.50	0.50	0.43
<u>Variety</u>									
Suwan 1	4.90 c	6.02 c	5.24 c	10.8 b	12.3 c	12.9 c	0.47 c	0.49 b	0.41 b
La Posta Sequia	5.39 b	6.62 b	5.66 b	11.5 b	13.6 b	13.6 b	0.49 a	0.49 b	0.42 b
KTX2602	4.74 c	6.16 c	5.51 b	9.8 c	12.8 c	12.6 c	0.50 a	0.49 b	0.45 a
DK888	6.64 a	7.56 a	6.39 a	13.5 a	14.5 a	14.8 a	0.51 a	0.52 a	0.43 a
<u>F-tests</u>									
Water regime (W)	***	*	**	***	**	***	***	***	***
N rate (N)	***	***	***	***	***	***	ns	ns	ns
Variety (Var)	***	***	***	***	***	***	***	***	***
W x N	***	ns	**	***	ns	***	ns	ns	ns
W x Var	ns	***	***	ns	*	ns	ns	***	***
N x Var	ns	ns	ns	ns	**	ns	ns	***	ns
W x N x Var	ns	ns	ns	ns	ns	ns	ns	ns	ns

*, **, *** significant at P=0.05, 0.01, 0.001, respectively. ns not significant.

[†] Means not followed by the same letter within a column are significantly different according to Fisher's protected LSD test at P=0.05.

Table 5: Main effects of water regime, rate of N application, and variety on traits related to kernel number in 1995, 1996 and 1997; results of *F*-tests for the effects of main factors and interactions

	Kernel number m ⁻²			Kernel row number per ear			Kernel number per row		
	1995	1996	1997	1995	1996	1997	1995	1996	1997
Grand mean	1910	2220	2160	13.0	13.3	13.3	24.7	27.9	26.8
<u>Water regime</u>									
Well-watered	2190 a [†]	2340 a	2370 a	13.3 a	13.5 a	13.6 a	27.4 a	29.2 a	28.1 b
Drought-stressed	1630 b	2120 b	1950 b	12.6 b	13.1 b	13.0 b	21.9 b	26.4 b	25.5 a
<u>N rate</u>									
0 kg N ha ⁻¹	1620 b	2150 b	1790 b	13.0	13.3	13.2	23.0 b	27.6	24.4 b
80 kg N ha ⁻¹	2030 a	2250 a	2300 a	13.1	13.3	13.3	25.2 a	27.9	28.1 a
160 kg N ha ⁻¹	2090 a	2290 a	2380 a	12.9	13.4	13.4	25.9 a	28.1	28.0 a
<u>Variety</u>									
Suwan 1	1700 c	1970 c	1960 c	14.1 a	14.5 a	14.4 a	22.0 c	25.3 c	24.6 d
La Posta Sequia	1900 b	2150 b	2080 b	12.9 c	13.0 b	13.3 b	25.4 b	29.2 a	27.6 b
KTX2602	1700 c	2180 b	2110 b	13.7 b	14.6 a	14.2 a	22.7 c	27.3 b	26.1 c
DK888	2340 a	2620 a	2490 a	11.1 d	11.2 c	11.5 c	28.6 a	29.6 a	29.2 a
<u>F-tests</u>									
Water regime (W)	***	*	**	**	**	***	***	*	**
N rate (N)	***	**	***	ns	ns	ns	***	ns	***
Variety (Var)	***	***	***	***	***	***	***	***	***
W x N	**	ns	*	ns	ns	ns	***	ns	ns
W x Var	ns	***	***	***	ns	ns	ns	*	ns
N x Var	ns	ns	ns	ns	ns	ns	*	ns	ns
W x N x Var	*	ns	ns	ns	ns	ns	*	ns	ns

*, **, *** significant at P=0.05, 0.01, 0.001, respectively. ns not significant.

[†] Means not followed by the same letter within a column are significantly different according to Fisher's protected LSD test at P=0.05.

4.1.2. Effects of Water Regime and N Rate on Yield Components

Both drought and low N supply reduced the number of kernels per unit ground area in all the years. The average reductions of number of kernels per unit ground area due to drought were 26% (1995), 9% (1996), and 18% (1997). The kernel number was significantly affected by the water regime x N rate interaction in 1995 and 1997 (Table 5). Under drought, increasing the rate of N application from 80 to 160 kg N ha⁻¹ did not stimulate the production of additional kernels. In contrast, the TKW increased with increasing rate of N application regardless of the water regime, but the differences between the 80 and 160 kg N treatments were generally small and significant in 1997 only (Table 7). The TKW of drought-stressed plants was considerably lower than that of well-watered plants; the average reductions due to drought were 9% (1995), 3% (1996), and 4% (1997) (Table 7).

Table 6: Effect of the rate of N application x variety interaction on the number of ears per plant in 1995, 1996, and 1997.

	Ears per plant		
	1995	1996	1997
0 kg N x Suwan 1	0.97	0.99	1.00
80 kg N x Suwan 1	1.06	1.03	1.05
160 kg N x Suwan 1	1.05	1.00	1.08
<i>F</i> -test	ns	ns	ns
0 kg N x La Posta Sequia	1.02	1.06	0.99 b [†]
80 kg N x La Posta Sequia	1.10	1.08	1.12 a
160 kg N x La Posta Sequia	1.12	1.07	1.12 a
<i>F</i> -test	ns	ns	**
0 kg N x KTX2602	1.01	1.01	1.03
80 kg N x KTX2602	1.04	1.03	1.09
160 kg N x KTX2602	1.01	1.05	1.12
<i>F</i> -test	ns	ns	ns
0 kg N x DK888	1.11 c	1.40 b	1.22 c
80 kg N x DK888	1.45 b	1.52 a	1.47 b
160 kg N x DK888	1.56 a	1.55 a	1.57 a
<i>F</i> -test	***	***	***

*, **, *** significant at P=0.05, 0.01, 0.001, respectively. ns not significant.

[†] Means not followed by the same letter within a column are significantly different according to Fisher's protected LSD test at P=0.05.

The number of kernels per unit ground area is the product of the number of ears per unit ground area, the number of kernel rows per ear, and the number of kernels per row. Drought significantly decreased (1995, 1997) or increased (1996) the ear number of only one variety, namely DK888 (Table 8). With increasing rate of N application, the frequency of subapical ear development of the semi-prolific hybrid DK888 increased significantly. The N effect was small and, as a rule, non-significant for the other varieties (Table 6), which explains the presence of significant N rate by variety interaction effects on the ear number in 1995 and 1997 (Table 7).

Table 7: Main effects of water regime, rate of N application, and variety on grain yield components in 1995, 1996 and 1997; results of *F*-tests for the effects of main factors and interactions

	Ears per plant			TKW (g)		
	1995	1996	1997	1995	1996	1997
Grand mean	1.13	1.15	1.15	279	296	262
<u>Water regime</u>						
Well-watered	1.14	1.13	1.19 a [†]	292 a	300 a	268 a
Drought-stressed	1.11	1.16	1.12 b	266 b	291 b	257 b
<u>N rate</u>						
0 kg N ha ⁻¹	1.03 b	1.12 b	1.06 b	263 b	287 b	248 c
80 kg N ha ⁻¹	1.16 a	1.16 a	1.18 a	284 a	298 a	267 b
160 kg N ha ⁻¹	1.19 a	1.17 a	1.22 a	291 a	302 a	272 a
<u>Variety</u>						
Suwan 1	1.03 bc	1.00 c	1.04 b	284	305 a	265 ab
La Posta Sequia	1.08 b	1.07 b	1.07 b	278	307 a	269 a
KTX2602	1.02 c	1.03 bc	1.08 b	275	283 b	261 bc
DK888	1.37 a	1.49 a	1.42 a	279	288 c	255 c
<u>F-tests</u>						
Water regime (W)	ns	ns	*	***	*	**
N rate (N)	***	*	***	***	***	***
Variety (Var)	***	***	***	ns	***	***
W x N	ns	ns	ns	ns	ns	ns
W x Var	**	*	***	ns	ns	***
N x Var	***	ns	***	ns	ns	***
W x N x Var	ns	ns	ns	ns	ns	ns

*, **, *** significant at P=0.05, 0.01, 0.001, respectively. ns not significant.

[†] Means not followed by the same letter within a column are significantly different according to Fisher's protected LSD test at P=0.05.

Drought stress before flowering reduced kernel row number by 5% in 1995, by 3% in 1996, and by 5% in 1997; while the differences between the water regimes were statistically significant (Table 5), there were no significant effects of N application on the kernel row number. Drought significantly reduced the kernel number per row by 3 (11%) in 1995, by 1.5 (4.5%) in 1996, and by 1.6 (4.8%) in 1997 (Table 5). The application of N fertilizer tended to increase (1996) or significantly increased (1995 and 1997) the number of kernels per row. Kernel number per row was significantly lower at N0 compared to N80 and N160; whereas there was no significant difference between the N80 and N160 treatments, neither under well-watered nor under drought stressed conditions.

4.1.3. Effects of Varieties on Grain Yield

In spite of the different yield levels in the various years, grain yield of the four genotypes hardly changed in terms of ranking. Averaged across the years and water regimes, the grain yield of the varieties decreased in the following order: DK888 (6.86 Mg ha⁻¹), La Posta Sequia (5.89 Mg ha⁻¹), KTX2602 (5.47 Mg ha⁻¹), and Suwan 1 (5.39 Mg ha⁻¹). Mean yield losses (percentages in brackets) due to drought were 1.60 Mg ha⁻¹ (26%) for KTX2602, 1.55 Mg ha⁻¹ (20%) for DK888, 1.40 Mg ha⁻¹ (21%) for La Posta Sequia, and 1.21 Mg ha⁻¹ (21%) for Suwan 1. In 1995 and 1997, the effects of the water regime by variety interactions on grain yield were significant (Table 4). The grain yield responses of the varieties to drought varied over the years (Table 10). The results are summarized as follows: Drought stress consistently led to greater yield losses for La Posta Sequia than for Suwan 1, but the losses in percent were about the same in all the years. Drought had a stronger effect on KTX2602 than on Suwan 1 in all the years, and it had a stronger effect on KTX2602 than on La Posta Sequia in 1995 and 1996, both in absolute and relative terms. The effects of water regime on DK888 varied considerable. While the relative loss in grain yield due to drought was similar in 1995 (31%) and 1997 (27%), the grain yield under pre-anthesis drought was almost the same as under continuous irrigation in 1996.

Drought decreased the kernel set of KTX2602 to a greater extent than that of Suwan 1 and La Posta Sequia in all the years (Table 8); the water regime by variety interaction was significant in 1996 and 1997 and non-significant ($P=0.47$) in 1995 (Table 5). The effect of the water regime by variety interaction on the kernel number per row was statistically significant in 1996 only (Table 5), but the P -values were also low in 1995 ($P=0.08$) and 1997 ($P=0.06$). The breakdown according to water regime revealed that the effect of water shortage on the kernel number was

consistently stronger for KTX2602 than for Suwan 1 and La Posta Sequia (data not shown).

The hybrid DK888 was very productive under well-watered conditions, at least in 1995 and 1997 when DK888 showed the strongest grain yield response to continuous irrigation. However, the water regime did not have a significant effect on the grain yield of DK888 in 1996 (Table 10). Under drought stress, DK888 produced 31% more grain than the mean of the other varieties in 1996; the corresponding figures were 34% in 1995 and 10% in 1997. Under well-watered conditions, DK888 out-yielded the other varieties by 12% (1996), 31% (1995), and 22% (1997).

DK888 was the top yielder in all three years (9.39 [1995], 8.06 [1996], and 8.44 [1997] Mg ha⁻¹ with 160 kg N ha⁻¹ under continuous irrigation). The average grain yield response to N application under continuous irrigation was weaker in 1996 than in 1995 and 1997 (Table 3), indicating that the availability of N was less limiting for grain yield in 1996 than in the other years.

Table 8: Effects of the water regime x variety interaction on ears per plant and kernel number in 1995, 1996, and 1997.

	Ears per plant			Kernel number m ⁻²		
	1995	1996	1997	1995	1996	1997
WW [†] x Suwan 1	1.00	1.01	1.06	1920	2090	2080
DS x Suwan 1	1.05	1.00	1.03	1480	1860	1840
<i>F</i> -test	ns	ns	ns	***	*	*
WW x La Posta Seq.	1.09	1.06	1.10	2140	2240	2260
DS x La Posta Seq.	1.08	1.08	1.04	1660	2050	1900
<i>F</i> -test	ns	ns	ns	***	ns	***
WW x KTX2602	1.01	1.03	1.08	2020	2410	2320
DS x KTX2602	1.04	1.02	1.08	1380	1940	1890
<i>F</i> -test	ns	ns	ns	***	***	***
WW x DK888	1.45	1.44	1.53	2670	2640	2810
DS x DK888	1.29	1.55	1.31	2010	2610	2170
<i>F</i> -test	***	**	***	***	ns	***

*, **, *** significant at P=0.05, 0.01, 0.001, respectively. ns not significant.

[†] WW = well-watered, DS = drought-stressed.

Table 9: Main effects of water regime, rate of N application, and variety on grain N, total shoot N, and shoot N concentration in 1995, 1996, and 1997; *F*-tests for the effects of main factors and interactions.

	Grain N kg ha ⁻¹			Total shoot N kg ha ⁻¹			Shoot N concentration g kg ⁻¹		
	1995	1996	1997	1995	1996	1997	1995	1996	1997
Grand mean	79.7	89.2	80.7	114.6	129.4	134.4	10.2	9.8	9.9
<u>Water regime</u>									
Well-watered	96.4 a [†]	93.5	90.8 a	142.4 a	137.3	154.8 a	9.5 b	9.3 b	9.5 b
Drought-stressed	62.9 b	84.8	70.6 b	86.8 b	121.4	114.0 b	10.7 a	10.3 a	10.3 a
<u>N rate</u>									
0 kg N ha ⁻¹	58.9 c	76.9 c	56.3 c	82.2 c	108.5 c	90.8 c	9.3 c	8.8 c	8.6 c
80 kg N ha ⁻¹	85.0 b	92.0 b	86.6 b	122.5 b	132.8 b	141.2 b	10.1 b	9.9 b	10.0 b
160 kg N ha ⁻¹	95.1 a	98.6 a	99.2 a	139.0 a	146.8 a	171.2 a	11.0 a	10.6 a	11.1 a
<u>Variety</u>									
Suwan 1	72.4 c	82.9 b	76.0 b	108.8 b	125.6	132.0	10.2 b	10.2 a	10.1 b
La Posta Sequia	79.9 b	91.1 a	80.6 a	115.1 b	132.5	137.0	10.0 c	9.8 b	10.0 b
KTX2602	74.7 bc	92.7 a	82.1 a	105.7 b	131.5	133.2	10.8 a	10.3 a	10.5 a
DK888	91.6 a	89.9 a	84.2 a	128.7 a	127.8	135.4	9.6 d	8.8 c	9.0 c
<u>F-tests</u>									
Water regime (W)	***	ns	**	***	ns	**	***	**	*
N rate (N)	***	***	***	***	***	***	***	***	***
Variety (Var)	***	**	**	***	ns	ns	***	***	***
W x N	***	*	**	***	**	***	ns	*	ns
W x Var	ns	**	ns	ns	ns	ns	ns	ns	ns
N x Var	ns	*	ns	ns	**	ns	ns	*	ns
W x N x Var	ns	ns	ns	ns	ns	ns	ns	ns	ns

*, **, *** significant at P=0.05, 0.01, 0.001, respectively; ns not significant.

[†] Means not followed by the same letter within a column are significantly different.

Table 10: Effects of the water regime x variety interactions on grain yield, harvest index, and anthesis-silking interval (ASI) in 1995, 1996, and 1997.

	Grain yield (Mg ha ⁻¹)			Harvest index			ASI (days)		
	1995	1996	1997	1995	1996	1997	1995	1996	1997
WW [†] x Suwan 1	5.82	6.43	5.73	0.41	0.47	0.38	0.0	0.6	0.1
DS x Suwan 1	3.98	5.61	4.74	0.53	0.51	0.44	6.0	2.5	0.4
<i>F</i> -test	***	*	**	***	***	***	ns	***	ns
WW x La Posta Seq.	6.38	7.08	6.3	0.43	0.47	0.39	(1.3)	(1.9)	(1.4)
DS x La Posta Seq.	4.40	6.16	5.02	0.54	0.51	0.45	0.1	0.2	(0.7)
<i>F</i> -test	***	**	***	***	***	***	***	***	*
WW x KTX2602	5.78	6.95	6.07	0.45	0.48	0.4	1.2	0.3	0.4
DS x KTX2602	3.71	5.37	4.94	0.54	0.49	0.49	4.3	2.6	2.0
<i>F</i> -test	***	***	***	***	**	***	***	***	***
WW x DK888	7.87	7.65	7.39	0.45	0.49	0.43	0.0	1.0	0.3
DS x DK888	5.40	7.47	5.39	0.56	0.55	0.44	1.1	1.8	1.0
<i>F</i> -test	**	ns	***	***	***	*	***	ns	**

*, **, *** significant at P=0.05, 0.01, 0.001, respectively. ns not significant.

[†] WW well-watered, DS drought-stressed.

4.1.4. Effects of Water Regime, N Rate, and Variety on Harvest Index

In 1995 and 1996, almost the same mean HI of 0.49 and 0.50 were found, whereas a clearly lower value of 0.43 was observed in 1997, averaged over all treatments (Table 4). While the N rate had no effect on the HI, water deficit before tasseling increased the HI in all the years. Drought stress before flowering increased the HI significantly ($P \leq 0.001$) in all years: from 0.44 to 0.54 in 1995, from 0.48 to 0.52 in 1996, and from 0.40 to 0.46 in 1997 (Table 4).

The mean HI of the OPVs was slightly lower than that of the hybrids. The HI response of the four genotypes to drought stress was almost identical in all three years. In 1995 and 1996, the HI of DK888 was significantly affected by N rate. It was above the average of the varieties at N80 and N160, but below at N0; the highest HI was found at N80 and N160 in 1995 when it was 0.56 (data not shown). In 1997, the HI response of DK888 was observed only under well-watered conditions; under drought, DK888 showed the lowest HI of all the varieties. In the same year, KTX2602 had the highest HI under drought. The water by variety interactions were highly significant ($P \leq 0.001$) in 1996 and 1997 (Table 10). In 1996, a significant N by variety interaction ($P \leq 0.001$) was

probably due to the fact that the stover DM of the varieties responded differently to N (data not shown).

4.2. Nitrogen Use Efficiency

4.2.1. Effect of Water Regime, N Rate, and Variety on Nitrogen Parameters

Total shoot N at maturity was significantly affected by the water regime in two years (1995, 1997), by the N rate in all the years, and by the variety in one year (1995) (Table 9). There were significant water regime by N rate interactions in all the experimental years (Table 9). Total shoot N increased with increasing availability of N, but the N effect was much stronger in the well-watered environment (Table 11). The effects of the other interactions on TSN were non-significant with the exception of the N rate by variety interaction in 1996 (Table 9). The breakdown according to variety revealed that the amount of shoot N increased as the rate of N application increased, but DK888 was much less responsive to N fertilization than La Posta Sequia (Table 13). A similar trend (the effect of the N rate by variety interaction was significant at $P=0.15$) was observed in 1997, but not in 1995 ($P=0.70$) (data not shown). At 0 kg N, DK888 had the largest amount of N in the tops (Table 13). This was observed in all the experimental years and under both water regimes (data not shown). It is, therefore, concluded that DK888 is especially efficient in accumulating N in the tops when little or no N fertilizer is applied.

Grain N was significantly affected by the water regime in two years (1995, 1997), by the N rate and the variety in all the years (Table 9). The decrease in grain N due to drought stress was greatest in 1995 (3.35 g m^{-2} ; $P \leq 0.001$), and smallest in 1996 (0.87 g m^{-2} ; $P=0.11$).

In all three years, the rate of N fertilization affected significantly the response of grain N to water regime. The water regime effect was significant at N80 and N160, but non-significant at N0 ($P=0.08$ in 1995 and $P=0.08$ in 1997; $P \geq 0.1$ in 1996). Averaged across the three N levels, the depression in grain N due to drought stress was significant for La Posta Sequia and KTX2602 ($P \leq 0.05$) and non-significant for Suwan 1 ($P=0.17$) and DK888 ($P=0.89$). There was a significant N rate by variety interaction in 1996: Contrary to the other varieties, DK888 on the unfertilized plots accumulated less N in the grain under well-watered conditions than under drought stress (8.0 g m^{-2} versus 8.2 g m^{-2}). Under N80 and N160, however, grain N of DK888 was slightly higher under continuous irrigation than under drought stress.

Table 1: Effects of the water regime x rate of N application interaction on grain yield (1995, 1996, 1997), amount of total shoot N (1995, 1996, 1997), grain and shoot N concentration (1996), N utilization efficiency (1996), and N harvest index (1996).

	Grain yield Mg ha ⁻¹			Total shoot N kg ha ⁻¹			Grain N conc. g kg ⁻¹		Shoot N conc. g kg ⁻¹		N utilization efficiency [†]		N harvest index [‡]	
	1995	1996	1997	1995	1996	1997	1996	1996	1996	1996	1996	1996	1996	1996
WW [§] x 0 kg N	4.68 b [¶]	6.59 b	4.84 c	93.2 c	111.6 c	101.1 c	11.9 c	8.2 c	59.1 a	0.70 a				
WW x 80 kg N	6.97 a	7.05 ab	6.83 b	151.9 b	138.1 b	158.4 b	13.6 b	9.2 b	51.6 b	0.70 a				
WW x 160 kg N	7.73 a	7.50 a	7.45 a	181.9 a	162.3 a	205.0 a	14.3 a	10.4 a	46.9 c	0.66 b				
F-test	***	**	***	***	***	***	***	***	***	***			**	
DS [‡] x 0 kg N	3.86	5.85	4.08 b	71.1 b	105.5 b	80.5 c	13.1 b	9.4 b	55.3 a	0.72 a				
DS x 80 kg N	4.64	6.35	5.44 a	93.0 a	127.4 a	124.1 b	14.1 a	10.5 a	49.5 b	0.69 b				
DS x 160 kg N	4.62	6.24	5.55 a	96.1 a	131.2 a	137.4 a	14.5 a	10.9 a	48.4 b	0.69 b				
F-test	ns	ns	***	**	***	***	***	***	***	***			*	

*, **, *** significant at P=0.05, 0.01, 0.001, respectively; ns not significant.

[†] grain yield / N in the shoot (g g⁻¹).

[‡] Grain N / total shoot N.

[§] WW well-watered; DS drought-stressed.

[¶] Means not followed by the same letter within a column are significantly different.

Averaged across the N rates and varieties, pre-anthesis drought resulted in a significant increase in NUtE in 1995 and a non-significant increase in 1997 (Table 14). In 1996, the mean NUtE was even slightly higher under continuous irrigation than under water deficit. However, the occurrence of significant water regime by N rate (1996), water regime by variety (1997), and water regime by N rate by variety (1997) interactions must be considered when interpreting the water regime effects on NUtE. In 1996, the NUtE was only higher in the well-watered than in the drought-stressed environment at 0 and 80 kg N, whereas it was lower at 160 kg N (Table 12). In 1997, the water deficit resulted in an increase in NUtE for three varieties (Suwan 1, La Posta Sequia, and KTX 2602), whereas the opposite was true for DK888 (Table 12). This was also found in 1996 when the effect of the water regime by variety interaction was significant at $P=0.08$, but not in 1995 ($P=0.70$).

Table 12: Effects of the water regime x variety interaction on grain yield (1995, 1996, 1997) and N utilization efficiency (1997).

	Grain yield Mg ha ⁻¹			N utilization efficiency [†]
	<u>1995</u>	<u>1996</u>	<u>1997</u>	<u>1997</u>
WW [‡] x Suwan 1	5.82 bc	6.43 c [§]	5.73 c	39.2 b
WW x La Posta Sequia	6.38 b	7.08 b	6.30 b	41.1 b
WW x KTX 2602	5.78 c	6.95 b	6.07 b	41.2 b
WW x DK888	7.87 a	7.65 a	7.39 a	50.1 a
<i>F</i> -test	***	***	***	***
DS [‡] x Suwan 1	3.98 bc	5.61 c	4.74 b	44.1
DS x La Posta Sequia	4.40 b	6.16 b	5.02 ab	44.5
DS x KTX 2602	3.71 c	5.37 c	4.94 b	45.2
DS x DK888	5.40 a	7.47 a	5.39 a	47.6
<i>F</i> -test	***	***	*	ns

*, *** significant at $P=0.05$ and 0.001 , respectively; ns not significant.

[†] Grain yield / N in the shoot ($g\ g^{-1}$).

[‡] WW well-watered; DS drought stressed.

[§] Means not followed by the same letter within a column are significantly different.

Table 13: Effects of the N rate x variety interaction on total shoot N (1996), N utilization efficiency (1996), N harvest index (1995, 1996, 1997), and apparent fertilizer N recovery (1996).

	Total shoot N kg ha ⁻¹		Shoot N conc. g kg ⁻¹		N utilization efficiency [†]		N harvest index [‡]		Apparent fertilizer N recovery [§]	
	1996		1996		1996		1995	1996	1997	1996
0 kg N x Suwan 1	104.3 ab [†]		9.1 a		54.6 b		0.69 b	0.70	0.60 b	--
0 kg N x La Posta Sequia	99.7 b		8.4 b		60.3 a		0.72 a	0.72	0.59 b	--
0 kg N x KTX 2602	114.2 a		9.6 a		51.9 b		0.74 a	0.72	0.67 a	--
0 kg N x DK888	115.9 a		8.3 b		61.8 a		0.73 a	0.70	0.64 a	--
F-test	*		***		***		**	ns	***	
80 kg N x Suwan 1	127.5 b		10.1 a		49.0 b		0.69 ab	0.67	0.61	34.6 a
80 kg N x La Posta Sequia	144.6 a		10.1 a		48.4 b		0.68 a	0.69	0.61	55.3 a
80 kg N x KTX 2602	128.8 b		10.5 a		46.1 b		0.72 a	0.71	0.63	15.9 b
80 kg N x DK888	130.2 b		8.8 b		58.7 a		0.71 a	0.70	0.63	16.8 b
F-test	*		***		***		*	ns	ns	***
160 kg N x Suwan 1	145.1		11.4 a		43.6 b		0.66 c	0.64 c	0.55 c	30.8
160 kg N x La Posta Sequia	153.2		10.8 a		45.1 b		0.70 ab	0.67 bc	0.58 bc	30.6
160 kg N x KTX 2602	151.4		10.9 a		44.2 b		0.69 b	0.70 ab	0.59 ab	23.0
160 kg N x DK888	137.4		9.4 b		57.8 a		0.72 a	0.71 a	0.61 a	14.0
F-test	ns		***		***		***	***	**	ns

*, **, *** significant at P=0.05, 0.01, 0.001, respectively; ns not significant.

[†] Grain yield / N in the shoot (g g⁻¹).

[‡] Grain N / total shoot N.

[§] (total shoot N of fertilized plants - total shoot N of unfertilized plants) / amount of fertilizer N applied x 100.

[†] Means not followed by the same letter within a column are significantly different.

Table 14: Main effects of water regime, rate of N application, and variety on N utilization efficiency, harvest index, and apparent fertilizer N recovery in 1995, 1996, and 1997; *F*-tests for the effects of main factors and interactions.

	N utilization efficiency [†]			N harvest index [†]			Apparent fertilizer N recovery [§]		
	1995	1996	1997	1995	1996	1997	1995	1996	1997
Grand mean	48.7	51.8	44.1	0.71	0.69	0.61	42.7	29.9	58.0
<u>Water regime</u>									
Well-watered	46.4 b [¶]	52.5	42.9	0.68 b	0.69	0.59 b	63.1 a	31.6	68.7 a
Drought-stressed	50.9 a	51.1	45.4	0.73 a	0.70	0.62 a	22.3 b	23.6	47.2 b
<u>N rate</u>									
0 kg N ha ⁻¹	52.5 a	57.2 a	50.0 a	0.72 a	0.71 a	0.62 a	--	--	--
80 kg N ha ⁻¹	48.2 b	50.6 b	43.8 b	0.70 b	0.69 b	0.62 a	50.1 a	30.6	64.8 a
160 kg N ha ⁻¹	45.2 c	47.7 c	38.6 c	0.69 b	0.68 b	0.58 b	35.3 b	24.6	51.1 b
<u>Variety</u>									
Suwan 1	46.7 c	49.1 c	41.7 b	0.68 c	0.67 b	0.59 b	43.6	32.7 a	56.6
La Posta Sequia	48.4 b	51.3 b	42.8 b	0.70 b	0.69 a	0.59 b	44.1	42.9 a	58.9
KTX2602	46.5 c	47.4 c	43.2 b	0.72 ab	0.71 a	0.63 a	37.3	19.4 b	52.7
DK888	53.0 a	59.4 a	48.8 a	0.72 a	0.70 a	0.63 a	45.9	15.4 b	63.7
<u>F-tests</u>									
Water regime (W)	**	ns	ns	**	ns	*	**	ns	*
N rate (N)	***	***	***	*	**	***	*	ns	**
Variety (Var)	***	***	***	***	**	***	ns	***	ns
W x N	ns	*	ns	ns	*	ns	ns	ns	ns
W x Var	ns	ns	***	ns	ns	ns	ns	ns	ns
N x Var	ns	***	ns	*	*	*	ns	***	ns
W x N x Var	ns	ns	*	ns	ns	**	ns	ns	ns

*, **, *** significant at P=0.05, 0.01, 0.001, respectively; ns not significant.

[†] Grain yield / N in the shoot (g g⁻¹).

[†] Grain N / total shoot N.

[§] (total shoot N of fertilized plants - total shoot N of unfertilized plants) / amount of fertilizer N applied x 100.

[¶] Means not followed by the same letter within a column are significantly different according to Fisher's protected LSD test at P=0.05.

The data for the three-way interaction in 1997 are shown in Table 15. The NUtE markedly decreased with increasing rate of N application in all the years (Tables 13 and 14). Averaged across the water regimes and N rates, DK888 exhibited the highest NUtE in all the years, while the ranking of the other varieties varied over the years (Table 13). There were some significant interactions (Table 14), but DK888 had the highest NUtE at almost all N and water levels (Tables 13 and 15).

Like as the grain DM, the total above-ground biomass production can be related to the amount of shoot N. The SNC was significantly higher under pre-anthesis drought than in the well-watered treatment in all the years (Table 9). In 1996, the SNC was significantly affected by the water regime by N rate interaction (Table 9), but the SNC was higher for drought-stressed than for well-watered plants at all the N levels (Table 11). The SNC increased with increasing rate of N application (Tables 9, 12, and 13). Averaged across the N rates and water regimes, the ranking of the varieties was identical in all the years (Table 9), but it depended on the N rate in 1996 (Table 13). On the other hand, DK888 consistently had the lowest SNC (Tables 9 and 13).

Averaged across the N rates and varieties, pre-anthesis drought significantly increased (1995, 1997) or tended to increase (1996) the NHI (Table 14). In 1996, the drought effect on NHI depended on the rate of N application; drought stress increased the NHI at 0 kg N, but decreased it at 160 kg N (Table 11). The NHI decreased as the rate of N application increased (Tables 9 and 14), but, as indicated by significant N rate by variety interactions (Table 14), the N effect was different for the varieties. In particular, the NHI of DK888 did not respond to N fertilization in 1995 and 1996 (Table 13). Averaged across the water and N levels, DK888 and KTX2602 had a higher NHI than Suwan 1 and La Posta Sequia in all the years (Table 14), but the breakdown according to the N rates (Table 13) and the various combinations of water regime and N rate (Table 15) revealed that the ranking of the varieties was variable.

Averaged across the varieties, pre-anthesis drought and high N fertilization resulted in a lower AFNR (Table 14). The ranking order of the varieties was identical in 1995 and 1996 (DK888 > La Posta Sequia > Suwan 1 > KTX2602), but DK888 showed a very low AFNR in 1996, irrespective of the N rate (Table 13).

Table 15: Effects of the water regime x N rate x variety interaction on N utilization efficiency and N harvest index in 1997.

	N utilization efficiency [†]	N harvest index [‡]
	1997	1997
WW [§] x 0 kg N x Suwan 1	42.9 c [¶]	0.56 c
WW x 0 kg N x La Posta Sequia	47.1 bc	0.59 bc
WW x 0 kg N x KTX2602	48.3 b	0.65 a
WW x 0 kg N x DK888	54.8 a	0.64 ab
<i>F</i> -test	***	***
WW x 80 kg N x Suwan 1	42.6 b	0.62
WW x 80 kg N x La Posta Sequia	40.1 b	0.57
WW x 80 kg N x KTX2602	41.0 b	0.6
WW x 80 kg N x DK888	50.8 a	0.62
<i>F</i> -test	***	ns
WW x 160 kg N x Suwan 1	32.0 b	0.51 b
WW x 160 kg N x La Posta Sequia	36.3 b	0.58 a
WW x 160 kg N x KTX2602	34.4 b	0.57 a
WW x 160 kg N x DK888	44.8 a	0.62 a
<i>F</i> -test	***	***
DS [§] x 0 kg N x Suwan 1	52.4 a	0.64 ab
DS x 0 kg N x La Posta Sequia	47.6 b	0.60 b
DS x 0 kg N x KTX2602	51.7 ab	0.68 a
DS x 0 kg N x DK888	54.9 a	0.64 ab
<i>F</i> -test	*	**
DS x 80 kg N x Suwan 1	41.2	0.6
DS x 80 kg N x La Posta Sequia	46.8	0.64
DS x 80 kg N x KTX2602	43.2	0.65
DS x 80 kg N x DK888	45.0	0.63
<i>F</i> -test	ns	ns
DS x 160 kg N x Suwan 1	38.8	0.59
DS x 160 kg N x La Posta Sequia	39.2	0.58
DS x 160 kg N x KTX2602	40.7	0.61
DS x 160 kg N x DK888	42.8	0.61
<i>F</i> -test	ns	ns

*, **, *** significant at P=0.05, 0.01, 0.001, respectively; ns not significant.

[†] Grain N / N in total shoot (g g⁻¹).

[‡] Grain N / total shoot N.

[§] WW well-watered; DS drought-stressed.

[¶] Means not followed by the same letter within a column are significantly different.

4.3. Grain Mineral Contents

4.3.1. Nitrogen and Minerals in the Whole Grain

With the exception of Ca and Cu, the concentrations of N and minerals in the grains were more or less the same in all years (Tables A3, A4, and A5). Averaged across the rates of N application and varieties, the grain N concentration in 1996 was lower under continuous irrigation than under drought stress (Table A4), but the opposite was true in 1995 and 1997 (Tables A3 and A5). The effects of N rate and variety on the grain N concentration were significant in all the cropping seasons. The existence of significant interactions must be considered when interpreting the results (Tables 9 and 16). The effect of the water regime by N rate interaction on the grain N concentration was significant in 1996 (Table 11), that of the water regime by variety interaction in 1996 and 1997 (Table 16), and that of the N rate by variety interaction in 1996 (Table 17). The water regime by variety interaction will be analysed in more detail, because it was significant in two of the three years (Table 16). In 1996, all the varieties had lower grain N concentrations under continuous irrigation than under drought stress; the effect of high soil moisture was least pronounced for DK888. In 1997, however, the grain N concentration of DK888 was affected to a greater extent by continuous irrigation than that of the other cultivars; only the grain N concentration of DK888 declined in the well-watered environment. The genotypic variation in the grain N concentration responses to different water regimes may merely reflect genotypic variation in the grain yield responses. Indeed, the positive effect of greater amounts of water on the grain yield was strongest for DK888 in 1997, while it was weakest for the same variety in 1996 (Table 12). Even though significant water regime by variety interactions occurred, the rank order of the varieties was similar: KTX2602 always had the highest and DK888 the lowest grain N concentration under both water regimes.

The concentration of minerals was not affected significantly by the water regime in either of the cropping seasons. Averaged across the water regimes and varieties, N fertilization brought about significant decreases in the concentrations of Ca and Zn in all the years (Tables A3 to A5). In contrast, N application significantly increased the concentration of Mn in 1996 and 1997 (Tables A4 and A5); a similar but non-significant response ($P=0.12$) was observed in 1995 (Table A3).

Averaged over the water and N fertilizer levels, the concentration of grain minerals was significantly affected by the variety, with the exception of K in 1995 and Ca in 1997 (Tables A3 and A5). There were some water regime by variety (Table 16) and N rate by variety (Table 17) interactions, while only one significant ($P=0.05$) three-way interaction (grain P concentration in

Table 16: Effects of the water regime x variety interaction on concentrations of grain N (1995, 1996, 1997), P (1997), K (1996), Mg (1997) and Cu (1996).

Water regime x variety	N		P [†]		K	Mg	Cu
	1995	1996	1997	1997	1996	1997	1996
	g kg ⁻¹						
Drought x Suwan 1	14.4 b*	14.1 b	14.0 a	3.33 b	4.07 a	1.14 b	2.68 a
Drought x La Posta Sequia	14.4 b	13.9 b	13.7 a	3.10 c	3.68 b	1.14 b	2.65 a
Drought x KTX2602	15.4 a	15.6 a	14.5 a	3.58 a	3.42 b	1.29 a	2.23 ab
Drought x DK888	13.5 c	12.0 c	13.5 a	3.15 c	3.70 b	1.15 b	1.92 b
F-test	***	***	*	***	***	***	***
Well-watered x Suwan 1	15.0 b	13.4 b	14.5 a	3.42 b	3.93 a	1.15 bc	2.65 a
Well-watered x La Posta Sequia	14.8 b	13.5 b	14.3 a	3.26 c	3.59 a	1.19 b	2.12 b
Well-watered x KTX2602	15.7 a	14.5 a	14.9 a	3.58 a	3.72 a	1.31 a	2.50 ab
Well-watered x DK888	13.8 c	11.8 c	12.6 b	3.15 c	3.56 b	1.14 c	2.10 b
F-test	***	***	***	***	**	***	***
F-test for the interaction	ns	*	**	*	*	**	***

*, **, *** significant at P=0.05, 0.01, and 0.001, respectively. ns not significant.

† Means not followed by the same letter within a column are significantly different.

‡ There was a significant (P=0.05) water regime x N rate x variety interaction.

1997, data not shown) occurred. In general, water supply and N level had a relatively weak impact on the relative performance of the varieties. For example, the breakdown of the data for P from 1997, according to variety, water regime, and the rate of N application revealed that KTX2602 and Suwan 1 had the highest and second-highest grain P concentrations under all combinations of water regime and N rate, while the other varieties differed only slightly (data not shown). Since the interactions were inconsistent over the years, they will not be discussed in detail.

Table 17: Effects of the N rate x variety interaction on concentrations of grain N (1996), P (1997) and Mn (1996).

	N	P [‡]	Mn
	g kg ⁻¹		µg kg ⁻¹
<u>N rate x variety</u>	<u>1996</u>	<u>1997</u>	<u>1996</u>
0 kg N x Suwan 1	12.9 ab [†]	3.33 b	6.17 b
0 kg N x La Posta Scquia	12.0 bc	3.18 a	5.61 b
0 kg N x KTX2602	14.1 a	3.58 a	7.80 a
0 kg N x DK888	11.3 c	3.17 b	6.26 b
<i>F</i> -test	***	***	***
80 kg N x Suwan 1	13.8 b	3.38 b	6.85 a
80 kg N x La Posta Scquia	14.3 b	3.11 c	7.32 a
80 kg N x KTX2602	15.4 a	3.61 a	7.99 a
80 kg N x DK888	11.9 c	3.05 c	6.08 b
<i>F</i> -test	***	***	***
160 kg N x Suwan 1	14.7 b	3.42 a	6.88 b
160 kg N x La Posta Scquia	14.8 ab	3.23 b	7.05 ab
160 kg N x KTX2602	15.8 a	3.56 a	8.35 a
160 kg N x DK888	12.4 c	3.23 b	6.69 b
<i>F</i> -test	***	***	***
<u><i>F</i>-test for the interaction</u>	***	*	*

*, *** significant at P=0.05 and 0.001, respectively. ns not significant.

[†] Means not followed by the same letter within a column are significantly different.

[‡] There was a significant (P=0.05) water regime x N rate x variety interaction.

The variety effects on the concentrations of grain N and minerals were as follows: averaged over the N rates and water regimes, KTX2602 had the highest concentrations of grain N, Mg, Ca, and Mn in all the years, Suwan 1 always had the highest concentrations of grain Zn and Cu, DK888 consistently showed the lowest concentrations of grain N, P, Mg, and Cu, and La Posta Scquia had the lowest grain Zn concentration in all the cropping seasons (Tables A3 to A5). In some cases,

variety interacted significantly with water regime and N rate, but the rank order of the varieties was similar under all water and N levels (Tables 13 and 17).

DK888 and Posta Sequia consistently produced higher grain yields than Suwan 1 and KTX2602 (Tables A3, A4, A5, and 11), which suggests that grain yield and concentrations of grain N and minerals are inversely related. The top yielder, DK888, lodged more N and minerals in the grain than all the other cultivars in 1995 (significant for N, P, K, Mg, Ca, and Zn). In 1996, the grain of DK888 contained the largest amounts of P, K, Mg, Ca, and Zn (significant for P, K, Mg, Zn), and, in 1997, the largest amounts of N, P, K, Mg, Ca, and Zn (significant for K and Zn) of all the tested varieties (data not shown). Thus, the low concentrations of grain N and minerals of DK888 were not due to the fact that this variety stored less N and minerals in the grain. Instead, the accumulation of large amounts of carbohydrates in the grain probably diluted these elements.

4.3.2. Nitrogen and Phosphor in Germ and Endosperm

Table 18 shows that the ratio of the endosperm to the germ DM was somewhat higher for KTX2602 than for DK888. The germ had higher concentrations of N and P than the endosperm, but the difference between these grain fractions was smaller for N than for P. KTX2602 had higher concentrations of N and P in both fractions than DK888. Analyses of germ and endosperm samples of KTX2602 and DK888 from the experiment in 1996 confirmed this result (KTX2602: germ N concentration, 31.6 g kg⁻¹; endosperm N concentration, 16.2 g kg⁻¹; germ P concentration, 25.4 g kg⁻¹; endosperm P concentration, 0.88 g kg⁻¹; DK888: germ N concentration, 31.0 g kg⁻¹; endosperm N concentration, 12.6 g kg⁻¹; germ P concentration, 21.8 g kg⁻¹; endosperm P concentration, 0.80 g kg⁻¹; the variety effects were statistically significant for all the traits except for the endosperm P concentration (P=0.08). The weighted mean N and P concentrations take the differences between the germ and endosperm dry weight into account. The calculated values agree well with the corresponding data in Table A3; the weighted mean concentrations of N and P were again higher for KTX2602 than for DK888. There were significant N rate by variety interactions for the mean N and endosperm N concentrations; the breakdown according to N rate revealed that the N concentration of KTX2602 increased to a greater extent in response to N fertilization than the N concentration of DK888. Table 17 shows a similar trend. Compared to KTX2602, the germ of DK888 contributed more N but less P (P=0.08) to the total amounts of N and P. In summary, KTX2602 did not have higher grain N and P concentrations than DK888 because the grains of the former variety contained relatively larger germs; rather, the differences were due to the higher N and P concentrations in both germ and endosperm.

Table 18: Effects of variety on the endosperm to germ dry matter ratio and on concentrations of N and P in endosperm and germ in 1995.

Variety	Endosperm/ germ dry matter ratio	concentration (g kg ⁻¹)						%	
		N in germ	N in endosperm	mean N, weighted	P in germ	P in endosperm	mean P, weighted	Germ N/ germ N plus endosperm N	Germ P/ germ P plus endosperm P
KTX2602	7.72	32.0 a [†]	14.1 a	16.20 a	23.5 a	1.07	3.68 a	23.3 b	74.3
DK888	7.97	30.8 b	11.0 b	13.20 b	20.1 b	1.00	3.14 b	26.2 a	71.8
F-test	ns	***	***	***	***	ns	***	***	ns
<i>F</i> -tests for the interactions									
Water regime x variety	ns	ns	*	ns	ns	ns	ns	ns	ns
N rate x variety	ns	ns	***	***	ns	ns	ns	ns	ns
Water regime x N rate x variety	ns	ns	ns	ns	ns	ns	ns	ns	ns

*, *** significant at P=0.05 and 0.001, respectively. ns not significant.

[†] Means not followed by the same letter within a column are significantly different.

5. DISCUSSION

5.1. Grain Yield

5.1.1. Effect of Water and N Rate on Grain Yield

The grain yield reductions from 13 to 32% (Table 4) over the years are well within the range of yield decreases due to pre-anthesis water deficit (Abrecht and Carberry, 1993; Claassen and Shaw, 1970; Eck, 1986; Hall et al., 1981; Lorens et al., 1987b; Nesmith and Ritchie, 1992; Weerathaworn et al., 1992b). Variations in the response of grain yield to drought among the experimental years mainly reflected variations in the duration and intensity of the drought. The accumulated ET_{crop} from emergence to 50% silking was 163 mm (1995), 154 mm (1996), and 175 mm (1997). This suggests that the drought stress was most severe in 1997 and least severe in 1996. In 1996, ample rain fell a few days before the scheduled end of the second drought phase. Thus, both relatively low ET and rain mitigated the effects of the drought treatment on grain yield. The second drought stress was somewhat shorter in 1997 than in 1995, because irrigation was resumed earlier. This explains why the differences in grain yield between drought-stressed and well-watered plants were smaller in 1997 than in 1995, even though the ET_{crop} until 50% silking was higher in 1997. The positive effects of adequate soil moisture on grain yield are amplified when sufficient N is available (see below). The amount of mineral N provided by the soil varied over the years, which must have contributed to the year-to-year variation in grain yield response to drought.

The significant water regime by N rate interaction effects on grain yield in 1996 and 1997 indicate that the grain yield increases resulting from N fertilization depended on the water regime. Similar effects were found in previous studies (Bennett et al., ; Eck, 1984; Eghball and Maranville, 1991; Knip and Mason, 1989; Pandey et al., 2000). Due to the low number of N treatments (three) and the limited range of N rates (0 to 160 kg N ha⁻¹) it is impossible to determine the exact N rates required for maximum grain yield under pre-anthesis drought and continuous irrigation. In the well-watered environment, an increase in the N rate from 80 to 160 kg N ha⁻¹ always brought about considerable increments in grain yield, suggesting that more than 160 kg N ha⁻¹ were required for maximum grain yield under adequate water supply. However, 80 kg N ha⁻¹ seem to have been enough to achieve maximum yield under pre-anthesis drought. According to Scharf et al. (2002) delaying the N application until late stages of vegetative development does not cause irreversible losses in grain yield, even when the symptoms of N stress were clearly visible. In farmers fields, a second N dose could, therefore, be delayed until just before the beginning of rapid vegetative growth, provided the fertilizer application is split into two. In dry years, the application of a second

N dose could be spared since it would be unlikely to increase grain yield.

5.1.2. Effects of Water and N Rate on Yield Components

Significant reductions in kernel number and, to a lesser extent, in TKW contributed to lower grain yields due to water shortage. In studies with US maize, it was also found that kernel number was the yield component most affected by pre-anthesis water deficit (Claassen and Shaw, 1970; Eck, ; Hall et al., 1981; Lorens et al., 1987b). The effects of drought on TKW were more distinct in this study than in that of Weerathaworn et al. (1992b), even though both studies were conducted on Farm Suwan in the dry season. NeSmith and Ritchie (1992) observed variable effects of drought on the TKW. They assumed that one source of variability of findings may be that very small kernels were discarded in some studies but not in others. There were few very small kernels in the present study, and they were retained in harvesting. Eck (1986) reported that the adverse effect of pre-anthesis drought on the kernel number was compensated for by an increase in TKW. Low TKW due to drought stress, as found in this experiments, may indicate that the plants were unable to fully meet the demand of the growing kernels. Since the long-term consequences of pre-anthesis drought include a smaller number of leaves, a smaller leaf area, and shorter internodes (Abrecht and Carberry, 1993; Hall et al., 1981; Nesmith and Ritchie, 1992; Siri, 1993), early drought stress probably reduced the capacity for the production and/or storage of assimilates during grain filling. However, pre-anthesis drought may also have affected the kernel size in a different way. The capacity of maize kernels to store assimilates is a function of the number of endosperm cells and starch granules established during the first 10 to 14 days after pollination (Commuri and Jones, 2001). Thus, reduced assimilate production due to a small green leaf area, reduced capacity to store assimilates due to short internodes, or high levels of endogenous abscisic acid (Mambelli and Stetter, 1998) during the above-mentioned critical period may have limited the TKW in this study.

The number of kernels per unit ground area is the product of the number of ears per unit ground area, the number of kernel rows per ear, and the number of kernels per row. The number of kernel-bearing ears is determined by genetic constitution and the environment (Motto and Moll, 1983). Like Balko and Russell (1980), Anderson et al. (1985), and Durieux et al. (1993), the frequency of subapical ear development of the semi-prolific hybrid DK888 increased with increasing rate of N application. The significant increase in ear number per plant for DK888 under drought stress in 1996 is surprising, because it was assumed that the ear number increases when the growing conditions improve. In line with this assumption, Hall et al. (1981) found that pre-anthesis drought reduced the number of subapical ears. On the other hand, Stanberry et al. (1963) reported

significant positive and negative effects of drought on the prolificacy of field-grown maize. In the greenhouse experiment of Dampney and Aspinall (1976), maize plants subjected to drought stress during early tassel development produced two to three mature ears, whereas unstressed plants formed a single ear. It was concluded that early drought stress can permanently affect the balance of correlative inhibition within the plant with a subsequent promotion of the growth of subapical ears. Thus, year-to-year variation in the severity of drought during certain early developmental stages may have caused the variable effects of moisture deficit on the ear number. However, another explanation will be presented in the section on variety effects.

In agreement with previous studies (Costa et al., 2002; Girardin et al., 1987), the kernel row number was unaffected by N supply. If the soil is very low in mineral N, however, application of N can increase the number of kernel rows (Schreiber et al., 1962). Weerathaworn et al. (1992b) and Siri (1993) found that pre-anthesis drought stress reduced the kernel row number, which is in line with the presented results, whereas Schreiber et al. (1962) did not obtain a significant increase in kernel row number from irrigation. This effect probably occurs only when the drought stress is early and severe, as it was especially in the years 1995 and 1997.

5.1.3. Effects of Varieties on Grain Yield

In 1995 and 1997, there were significant water regime by variety interactions for grain yield. This was expected for two reasons. First, La Posta Sequia (C4) is a product of CIMMYT's breeding programme for drought tolerance. The CIMMYT breeders select for a shorter ASI, because this trait is associated with high grain yield under drought (Edmeades et al., 2000). This explains why La Posta Sequia had the shortest ASI in this study (Tables 7 and A2). La Posta Sequia (C4) performs well under drought (Edmeades et al., 2000), but the drought stress treatments of CIMMYT clearly differ from that in this study (see 'Introduction'). This may explain why La Posta Sequia did not outyield the local check variety, Suwan 1, under pre-anthesis drought stress. Second, it was conceivable that KTX2602, the earliest variety, was at the greatest risk of yield loss under drought, because irrigation was resumed only a few days before 50% tasseling of this variety, but five to six days before 50% tasseling of the other varieties. Two of the after-effects of pre-anthesis drought are a delay of silk extrusion and a longer ASI (Hall et al., 1982; Nesmith and Ritchie, 1992; Weerathaworn et al., 1992b). The ASI of a given cultivar increases with increasing severity of stress (Hall et al., 1982). As assumed, the ASI of KTX2602 was average in the well-watered environment but was longest when water was in short supply (Table 10). The effect of the water regime by variety interaction on the ASI was statistically significant in all the years (Table

A2). These results strongly suggest that KTX2602 suffered most from a pre-anthesis moisture deficit. Furthermore, the effect of water shortage on the kernel number was consistently stronger for KTX2602 than for Suwan 1 and La Posta Sequia. Similarly, drought reduced the kernel number per row of KTX2602. Although this effect was statistically significant in 1996 only, the P-values of 1995 and 1997 were also low. Thus, there is strong evidence that drought affected the kernel set and grain yield of KTX2602 to a greater extent than that of Suwan 1 and La Posta Sequia, because KTX2602 was the earliest variety.

Like in the study of Manupccrapan et al. (1997), it was found that DK888 was very productive under well-watered conditions, at least in 1995 and 1997 when DK888 showed the strongest grain yield response to continuous irrigation. However, the water regime did not have a significant effect on the grain yield of DK888 in 1996 (Table 10). The results of 1996 can be interpreted in two ways: (i) DK888 was more tolerant to drought than the other varieties, possibly because prolific hybrids are less susceptible to moisture stress than single-cared hybrids (Thomison and Jordan, 1995); (ii) DK888 may not have realized its full yielding potential in the well-watered environment, because factors other than soil moisture limited grain yield. We strongly support the latter explanation, since the relative yield performance of DK888 in 1996 under drought was not particularly good, but exceptionally poor in the well-watered environment (Table 10). DK888 was the top yielder in all three years (9.39 [1995], 8.06 [1996], and 8.44 [1997] Mg ha⁻¹ with 160 kg N ha⁻¹ under continuous irrigation). In contrast to the yield levels under well-watered conditions of Suwan 1, KTX2602, and La Posta Sequia, which were clearly higher in 1996 than in 1995 and 1997, DK888 produced the lowest maximum grain yield in 1996 (Table 10). The average grain yield response to N application under continuous irrigation was weaker in 1996 than in 1995 and 1997 (Table 3), indicating that the availability of N was less limiting for grain yield in 1996 than in the other years. Consequently, the low maximum yield of DK888 in 1996 was not due to N deficiency. Rather, the observations suggest that environmental factors other than water and N limited the grain yield of well-watered DK888 in 1996.

The soil was low in some mineral nutrients (see Materials and Methods), which may have limited the grain yield of the top yielder, DK888, in 1996. On the other hand, the maximum grain yields were higher in 1995 and 1997 (see above), even though the maize was grown on adjacent areas on the same experimental field. We assume that the yielding potential of well-watered DK888 was not tapped in 1996 because of unfavourable weather and climatic conditions. DK888 had the same biomass at flowering as KTX2602 and La Posta Sequia under both water regimes (data not shown). Thus, the factors that limited the grain yield of well-watered DK888 in 1996 were

effective around flowering or later. Under continuous irrigation, 50% silking of DK888 was reached on 24 February in 1996. The silk of the subapical ears of unstressed plants usually emerges about one or two days after that of the apical ear (Hall et al., 1982; Harris et al., 1976; Sarquis et al., 1998), so that 50% silking of the subapical ears probably occurred on 25 or 26 February. After 50% silking of the apical ears, the following days were relatively cloudy, which reduced the daily irradiation by 10% to more than 50% compared to clear days (data not shown). At the same time, the wind velocity was fairly low, and the temperatures were thus relatively high (more than 31°C maximum air temperature). High maize yields seem to be associated with relatively low temperatures and high solar radiation (Muchow, 2000). Evans (1993) linked the low yields of maize in tropical environments to the low photothermal quotient, i.e. the low ratio of solar radiation to temperature. The adverse effects of low light intensity on kernel production and grain yield are most severe around flowering (Fischer and Palmer, 1984). Thus, the combined effects of relatively high temperatures (high demand of the florets for assimilates per unit time), low light intensity (low production of assimilates per unit time), and short days (low production of assimilates per day) right after 50% silking may have limited the production of photosynthates, thus increasing the abortion rate of pollinated florets of DK888. Earley et al. (1966) demonstrated that reducing the assimilate supply to maize through shading predominantly eliminated the subapical ears. Ovaries on the second ears of stressed maize plants are fertilized (Harris et al., 1976) but are aborted shortly after flowering (Prine, 1971). If the above arguments are correct, then the unfavourable environmental conditions shortly after 50% silking in 1996 would have caused extensive abortion, in the first instance, of the subapical ears. Indeed, in contrast to 1995 and 1997, the number of ears per plant in 1996 was significantly higher for drought-stressed than for well-watered plants (Table 8). The extent to which low light supply around flowering decreases the grain yield can depend on the variety (Fischer and Palmer, 1984). It may be that the unfavourable environmental conditions shortly after 50% silking in the 1996 experiment did not cause a reduction in the grain yield of the other varieties, because the number of kernels was limited by factors other than the availability of assimilates, for example, by the abortion of late pollinated florets through hormone-mediated dominance signals (Carcova et al., 2000). The temperatures around silking were not high enough to have an adverse affect on the viability of the pollen (Schoper et al., 1986).

5.1.4. Effects of Water Regime, N Rate, and Variety on Harvest Index

The lowest mean HI of continuously irrigated maize was found in 1997 when the total DM was higher and the grain yield lower than in the other years. Very dry plants were harvested in 1995

and 1996, whereas in 1997 the plants were more moist and, therefore, less brittle at the harvest. Thus, differences in the extent of leaf shedding and in the loss of leaf material during collection and processing may have contributed to the between-year variation in the total biomass and HI. The kernel number was average in 1997 (Table 5), while the TKW was low, irrespective of the water regime (Table 7). This suggests that insufficient assimilate supply during grain filling limited kernel size. On the other hand, the total biomass production in the well-watered environment was high in 1997. Thus, the allocation of assimilate to the growing grains may have been inefficient in 1997. It is also possible, however, that unfavourable conditions during the establishment of the number of endosperm cells and starch granules limited the kernel size. The weather data give no indications as to why the TKW was low in 1997.

Early drought increased the HI in all the years, similarly to reports for temperate (Lorens et al., 1987b) and tropical (Siri, 1993) maize (Table 4). In a previous dry season experiment on Farm Suwan, the HI of irrigated tropical maize hybrids ranged from 0.39 to 0.43; in a rainy season experiment with the same set of hybrids, the HI varied from 0.31 to 0.38. In the former experiment, the HI of early maturing European hybrids was as high as 0.53 (Feil et al., 1992b), suggesting that the low HI of tropical maize is genetically determined, at least in part. Hay and Gilbert (2001), too, reported that the HI of tropical maize can exceed 0.5. In comparing these results with those of other studies, however, it must be taken into account that the experiments were conducted 1150 m above sea level.

5.2. Nitrogen Use Efficiency

5.2.1. Effects of Water Regime, N Rate, and Variety on Nitrogen Parameters

Pre-anthesis drought consistently reduced the amount of TSN, but the adverse effect of water deficit on shoot N was much more distinct under high N fertilization (Table 9). In contrast, Eghball and Maranville (1991) found no statistically significant effects of the water regime and the water regime by N rate interaction on TSN, but drought stress tended to reduce the accumulation of N in the tops. Unfortunately, the authors did not report any information about the time, duration, and intensity of stress so that the nature of drought stress remains unclear. The data for total plant DM at tasseling indicate that the drought stress before anthesis was very mild. Bennett et al. (1989) found that pre-anthesis water deficit resulted in a non-significant decrease in total plant N. The water regime by N rate interaction had a sizable impact on accumulation of N in shoots, but no information about the statistical significance of the water regime by N rate effect was provided.

In agreement with Moll et al. (1982), Eck (1984), Eghball and Maranville (1991), Lafitte et al. (1997), and Akintoye et al. (1999), the NUtE decreased as availability of N increased (Table 13). However, especially the data presented in the Tables 3 and 5 indicate that it is not advisable to generalize about the effects of N fertilization on the NUtE. The existence of genotypic variation in NUtE is well established (Akintoye et al., 1999; Anderson et al., 1984, 1985; Eghball and Maranville, 1991; Lafitte et al., 1997; Machado and Fernandez, 2001; Moll et al., 1982). In the study of Eghball and Maranville (1991), the water regime by variety and water regime by N rate by variety interactions were non-significant at the $P=0.10$ level, leading the authors to state that this could greatly simplify the selection of maize genotypes for NUtE. There were also significant differences in NUtE among the varieties in this study. Despite a few sporadic interactions (Table 13), DK888 had always the highest NUtE (Tables 9, 14, and 15). This indicates that genotype differences in NUtE are fairly stable over years, water regimes, and N levels.

Like in other experiments (Moll et al., 1987), genotypic variation in the SNC was found. Even though a significant N rate by variety interaction occurred in 1996 (Table 9), the data in Tables 9 and 14 suggest that year, water regime, and N supply and the interactions between water regime and N supply had a limited impact on the ranking of the varieties. Lafitte et al. (1997) reported that improved varieties had a lower SNC than landraces, irrespective of the level of N supply. In agreement with this, the top yielder in the experiment, DK888, always had the lowest SNC (Tables 9 and 13). Eghball and Maranville (1991) used the reciprocal value of the SNC ($\text{g shoot DM g}^{-1} \text{ shoot N}$) as an indicator of NUtE and found no significant effect of the water regime on this trait.

In other dry season experiments on Farm Suwan, the NHI of tropical varieties ranged from 0.65 to 0.75 (Feil et al., 1992b), from 0.53 to 0.64 (Feil et al., 1993), and from 0.55 to 0.68 (Feil et al., 1993), while the NHI of European early maturing germplasm ranged from 0.66 to 0.76 (Feil et al., 1992b). In the present study, there were consistent genotypic differences in NHI (Table 14), but the ranking of the varieties was not stable across the various levels of water and N supply (Tables 10 and 15). Application of N fertilizer had no significant effect on the NHI in three other experiments carried out on Farm Suwan (Thiraporn et al., 1992). In contrast, there were significant N rate effects and significant N rate by variety interactions in this study (Table 13). The mean NHI varied from year to year; especially low values were found in 1996 (Table 14). Very dry plants were harvested in 1995 and 1996, whereas in 1997 the plants were more moist and, therefore, less brittle at the harvest. Thus, differences in the extent of leaf shedding and in the loss of leaf material during collection and processing may have contributed to the between-year variation in the NHI. As expected from literature reports (Schindler and Knighton, 1999), high fertilization was

associated with low AFNR (Table 14). In a well-irrigated dry season experiment conducted on Farm Suwan, the mean AFNR of 16 varieties was 62.4% at 40 kg N ha⁻¹, 58.7% at 80 kg N ha⁻¹, and 44.3% at 160 kg N ha⁻¹ (Feil; unpublished data). The stability of the ranking of the varieties over the years suggests that genotypic variation in AFNR existed in the present study. The exceptionally low AFNR of DK888 in 1996 resulted from the fact that DK888 accumulated more N in the tops than the other varieties on the unfertilized plots, but accumulated about the same (in the 80 kg N treatment) or even lower (in the 160 kg N treatment) amounts of N in the shoots on the fertilized plots (Table 14). Feil et al. (1993) used the isotopic method to estimate the recovery of fertilizer N, which was applied at planting and tassel emergence; no significant differences in fertilizer N recovery were found among the six tropical varieties under investigation.

5.2.2. Breeding for Nitrogen Use Efficiency

In the following, the value of NUtE, SNC, NHI, and AFNR as breeding traits will be discussed critically. All these indicators of N efficiency involve the uptake of N. Most investigators equate N uptake with the amount of N in the tops. This is not quite correct, however. First, a significant portion of the N in mature maize plants is located in the roots. Second, the amount of shoot N at maturity is the final result of N absorption from the soil and air and the loss of N. The pathways of N loss from shoots include processes such as leaf shedding, emission of ammonia and other nitrogenous gases, leaching of nitrogenous compounds in the rain etc. (Feil, 1997; Wetselaar and Farquhar, 1980). Francis et al. (1993) applied ¹⁵N tagged N fertilizer at rates from 50 to 300 kg N ha⁻¹ to irrigated field-grown temperate maize and estimated that the post-anthesis N losses from the tops ranged from 45 to 81 kg N ha⁻¹. In a study with hydroponically grown maize, N removed from the nutrient solution was never fully recorded in the maize plants. The percentage of N recovery varied among the genotypes tested, demonstrating that maize varieties may differ in total N loss (Chevalier and Schrader, 1977). These and other reports (Karlen et al., 1988; Weiland and Ta, 1992) suggest that, in this experiments too, a significant portion of the N absorbed by the plants from the soil was lost later in the season. Furthermore, the varieties may have differed in the extent of N loss from their tops.

Several physiological traits that may contribute to a more efficient utilization of plant N have been put forward (Hirel et al., 2001; Sinclair and Vadez, 2002). But should maize breeders really select for high NUtE, low SNC, and high NHI? The answer to this question mainly depends on the demands on product quality. Maize grain produced in the developing countries is, for a large part, used as staple food. Even though the nutritive value of ordinary maize protein is low for

non-ruminants, high levels of protein in the grains may help avert protein deficiency in the poorer sectors of the population. Furthermore, subsistence farmers may need maize stover as a feed supplement to enhance the protein supply to ruminant livestock. Selection for high NUtE or low SNC will lead to varieties that have low N concentrations either in the stover or in the grain, or in both components. In this study, the top yielder, DK888, had the lowest concentrations of N in the stover and the grains. Thus, breeding for high NUtE or low SNC is not advisable if the maize is directly or indirectly consumed by humans who are at risk of protein deficiency. Theoretically, the concentration of protein in the grain can be increased by selecting for a higher NHI, provided that the DM HI and the TSN are maintained. However, this breeding strategy will necessarily result in decreases in the concentration of stover protein, thus affecting the nutritive value of the stover for protein deficient ruminant livestock. In industrialized countries, the bulk of the maize grain produced or imported is used for animal feed. The concentration of protein is of minor importance because of the ready availability of inexpensive, high quality protein supplements. Thus, the adverse effects of selecting for high NUtE or low SNC on product quality would be of limited relevance. The same is true if the maize is used as fuel or raw material for industrial purposes. However, one-sided breeding for high NUtE may lead to genotypes that exhibit a low N uptake efficiency, thus increasing the risk of N loss from the soil to the environment. It may be that the scope for genetically increasing the N uptake is limited under low-N conditions (Feil, 1997). Incorporation of traits which enhance the NUtE into existing high-yielding germ plasm would at least increase the carbohydrate yield on low-N soils. The protein requirements of humans and livestock must then be met by alternative sources, e.g. by legumes. Should breeders select for high AFNR? Varieties show a high AFNR when (i) large amounts of fertilizer N are accumulated in the tops or (ii) medium amounts of fertilizer N are accumulated in the tops while the amount of shoot N on the unfertilized reference plots is small. Thus, selecting for high AFNR may lead to varieties that show a medium fertilizer N recovery, but are inefficient in N uptake under low-N conditions. It is concluded that, when selecting for high AFNR, the performance of the genotypes in terms of N uptake on unfertilized land should also be considered.

5.3. Grain Mineral Contents

5.3.1. Effect of Water Regime and N Rate on Grain Mineral Content

Except for Ca in 1995, the mean concentrations of the minerals in the three experiments (Tables A3 to A5) are similar to those reported by Watson (1987). According to Pietz et al. (1978), Miller

(1958) reported Ca concentrations as high as 1100 g in maize grains, indicating that the mean Ca concentration found in 1995 (136 g) is not uncommon. Even though continuous irrigation markedly increased the grain yield in all the cropping seasons (Tables A3 to A5) and, thus, the grains' demand for minerals, there was no decrease in the concentrations of grain minerals. It has been reported that drought can alter the root DM (Eghball and Maranville, 1993) and the partitioning of roots to upper soil layers and to the subsoil (Klepper, 1991). In his experiments with maize on Farm Suwan, Camp (1996) found that the zone of maximum water uptake shifted down the soil profile with increasing drought stress. This suggests that the drought-stressed plants in the present experiment obtained water and minerals from the subsoil, where the concentrations of plant-available nutrients were generally low (see 'Materials and Methods'). Nevertheless, concentrations of grain minerals were not affected by the water regime in either year. This finding is in line with the results of Harder et al. (1982), who, however, studied the effects of post-anthesis drought on the concentrations of grain P and K.

Water regime significantly affected the grain N concentration, at least in 1996 (Table A4). Comparable responses of grain protein to irrigation have also been reported by Jurgens et al. (1978), Harder et al. (1982), and Kniep and Mason (1991). However, the results in 1995 (Table A3) and 1997 (Table A5) demonstrate that it is impossible to generalize about the impact of drought stress on the level of grain protein. The drought stress was much more severe in 1995 and 1997 (Tables A3 and A5) than in 1996 (Table A4), as indicated by the large increments in grain yield due to continuous irrigation in the former years. Nevertheless, grain N was not diluted, i.e. continuous irrigation brought about similar increases in grain yield and grain N yield.

Application of N fertilizer brought about significant increases in grain yield (Tables A3, A4), thus increasing the amount of minerals required by the grains to maintain the concentration. A greater demand of the grains for minerals can be met when the plants take up larger amounts of nutrients from the soil. Some studies indicate that heavy N fertilization may reduce root growth (Durieux et al., ; Eghball and Maranville, 1993; Oikeh et al., 1999). If this is true, it might be difficult for the plants to acquire adequate amounts of mineral nutrients when N is applied at high rates. Nevertheless, even when the rates of N fertilization were high, the concentrations of most of the mineral nutrients in the grain did not decrease in the experiments (Tables A3 to A5). The heavily fertilized plants, probably, exploited the mineral nutrient reserves in the stover more efficiently. Former research in Thailand showed that the P harvest index (= proportion of grain P to total shoot P) increased as the rate of N application increased (Thiraporn et al., 1992). In these experiments, N fertilization consistently resulted in a decrease in the concentrations of grain Ca and Zn and in an increase in the concentration of grain Mn (Tables A3 to A5). Pietz et al. (1978) found

significant positive correlations of N rate and grain Mn concentration on four of nine research fields. Significant negative correlations between N rate and Ca were found on three of the fields, while a significant positive correlation was observed on one field. Application of N usually decreased the concentration of grain Zn, but the correlation was significant on three fields only. A dilution effect due to a higher grain yield as a result of N fertilization may have contributed to the inverse relationship between N rate and the concentrations of Ca and Zn in the experiment (Tables A3 to A5). The effect of N fertilization on the mineral composition of plant tissues may depend on the N form. We applied ammonium sulfate, which acidifies the soil. Application of ammonium rather than nitrate is considered to be advantageous on neutral to slightly alkaline soils, because it enhances the availability of Zn and Mn to the crop (Schnug and Finck, 1980). Consequently, changes in the soil pH may explain why N fertilization led to higher concentrations of grain Mn. In the case of Zn, the dilution effect caused by increments in grain yield may have been stronger than the ammonium effect.

5.3.2. Effect of Variety on Grain Mineral Content

The top yielder, DK888, had lower concentrations of N and many mineral elements in the grain than the other varieties tested (Tables A3 to A5). At the same time, DK888 stored large amounts of N and minerals in the grain. Thus, the relatively low concentrations of grain minerals and N for DK888 seem to be due to a dilution effect. Does breeding for grain yield tend to lower the levels of grain protein and minerals? In previous studies on Farm Suwan with 12 to 16 tropical maize varieties, the relationship between grain yield and the concentrations of grain P, K, and N was not inverse (Feil et al., 1993; Feil et al., 1990). In agreement with this, grains of old and modern maize hybrids marketed in Ontario showed no clear differences in the concentrations of these elements, but the concentrations of grain Mg, Cu, Mn, and selenium (Se) tended to be higher in the old varieties than in newer ones (Vyn and Tollenaar, 1998). However, genetic progress in the grain yield of US maize was associated with a significant drop in the concentration of grain N (Duvick and Cassman, 1999). Likewise, improved tropical varieties had lower concentrations of N in the grain than landrace varieties, irrespective of the level of N supply (Lafitte et al., 1997).

There were some significant water regime x variety (Table 16) and N rate x variety (Table 17) interactions, but they were inconsistent across the years. The same was true for the one three-way interaction. The breakdown according to water regime (Table 16), rate of N application (Table 17), and the various combinations of water regime and N rate revealed that the water regime and the rate of N fertilization had a small impact on the ranking of the varieties. It is, therefore, concluded that varietal differences in the concentrations of grain N and minerals are fairly stable across wide

ranges of water and N supply.

The germ contains about 78% of the minerals in the kernels and 18% of the protein (Watson, 1987). It is hypothesized that differences in the composition of minerals in the grains of KTX2602 and DK888 reflect a variation in the proportions of germ and endosperm DM to total kernel weight. Watson (1987) reported that endosperm and germ made up on average 82.9% (range 81.8 to 83.5%) and 11.1% (range 10.2 to 11.9%) of the whole kernel dry weight of dent maize kernels of seven US hybrids. Thus, the mean ratio of endosperm to germ dry weight was about 7.5. Somewhat higher values were found for KTX2602 (7.7) and DK888 (8.0) (Table 18). The results demonstrate that KTX2602 and DK888 did not differ in the concentrations of grain N and P because KTX2602 had a larger germ and smaller endosperm than DK888. Rather, the N and P concentrations were higher for KTX2602 in both kernel fractions.

6. CONCLUSIONS

6.1. Drought Stress

The results show that varieties can respond individually to different water regimes. There is, however, little evidence that the variations in the grain yield response to drought were due to variations in physiological traits that co-determine tolerance to pre-anthesis drought. Instead, differences in the speed of development and environmental factors, which limit the yielding potential under well-watered conditions, seem to contribute to the effects of the variety by water regime interactions on grain yield. It is assumed that early varieties are, in general, more affected by long-lasting pre-anthesis drought spells, in particular when the period between the end of the drought period and the beginning of flowering is short. The careful management of the applied stress in terms of severity and timing is a prerequisite for a successful breeding programme for drought tolerance. Most of the cited experiments on drought tolerance were conducted under dry-season conditions. The low yield of DK888 in the well-watered experiment of 1996 suggests that it is important to study the influence of the meteorological and phytopathological conditions of the rainy season and to compare them with the effects of the dry season.

The selection programme for drought tolerance at CIMMYT targets an ideotype that yields well under severe drought stress, starting before silking, and moderate drought stress from late flowering and throughout grain filling (Edmeades et al., 2000). Since these drought stress treatments clearly differ from that in this study, it is not surprising that the CIMMYT variety La Posta Secuía, compared to the other tested varieties, did not show a smaller yield reduction under drought stress. Nonetheless, La Posta Secuía was competitive under continuous irrigation in Thailand, even though it was selected under severe drought in Mexico. In the rainy season, however, prevalent downy mildew (*Peronosclerospora sorghi*) infestation may adversely affect the relative yield performance of La Posta Secuía. The outcome of the study indicates that a separate breeding programme for tolerance to pre-anthesis drought is necessary. This and the fact that pre-anthesis drought is wide-spread throughout sub-tropical regions should lead breeders to pay more attention to this form of drought stress.

Pre-anthesis water deficit affects the kernel set and, to a lesser extent, the mean kernel weight. The latter suggests that the kernel size is limited by an inadequate assimilate supply to the growing grain. The assimilate supply to the grain may increase if varieties are bred with an enhanced photosynthetic capacity during grain filling. However, this breeding strategy is doomed to failure if pre-anthesis drought limits the kernel size by reducing the number of endosperm cells and starch

granules. Both kernel weight and kernel number might increase if varieties are developed, the roots of which rapidly penetrate the soil and exploit the water resources in deep soil layers. Ideally, breeders should manipulate the roots so that their total biomass does not change. Pre-anthesis drought can increase the HI of tropical lowland maize to 0.56, but the HI of well-watered tropical maize is low compared with that of temperate maize. Breeding for a higher HI while maintaining the total above-ground biomass may conflict with the interests of subsistence farmers, who require large amounts of high-quality stover.

6.2. Nitrogen Deficiency

When maize is subjected to pre-anthesis drought, 80 kg N ha⁻¹ is sufficient to achieve the maximum grain yield, whereas more than 160 kg N ha⁻¹ seem to be required on moist soils, independent of the variety. We recommend that such high doses of N fertilizer be split, whereby the second N dose should be delayed until just before the beginning of rapid vegetative growth. This would significantly reduce the risk of nitrate leaching on intensively irrigated land and after heavy rainfall. According to Scharf et al. (2002), delaying the N application until late stages of vegetative development did not cause irreversible losses in grain yield of temperate maize, even when the symptoms of N stress were clearly visible. In dry years, however, the farmer may decide against applying the second N dose, because additional N is unlikely to result in economic increases in grain yield.

The existence of variety by N and N by water regime interactions demand a carefully managed N regime and the precise observation of the N mineralisation of the field. The latter is especially true for N-depleted soils and at the beginning of the season, when, depending on factors such as soil moisture, temperature and organic N content, sufficient N_{min} may be supplied to the plants, so that the yielding potential of drought-affected plants is not limited. The low soil fertility in tropical fields raises the question of where research and breeding programmes with tropical maize should be conducted. Selection on fertile soils of experimental stations could lead to a loss of useful genetic variation in the tolerance to low N availability. Since it has been shown in several experiments that breeding for drought tolerance simultaneously improves the potential yield of genotypes under low N, it might be wise to focus on the improvement of drought tolerance, especially in national breeding programmes of developing countries with limited resources.

Parameters such as N uptake efficiency and AFNR, indicators of N efficiency, involve the uptake

of N. However, a significant portion of the N absorbed from the soil by the plants may remain in the roots or be lost later in the season. Furthermore, N that has accumulated in the plant tissue can be lost at harvest. Because the real total N uptake is unknown, it is suggested that 'shoot N' or 'apparent N uptake' should replace the term 'N uptake'. Physiological traits, which may contribute to the more efficient utilization of plant N are NUtE, low SNC, and high NHL. However, genotypes with improved NUtE might not be desirable, depending on how the plant products are used. Especially in developing countries, where maize is a staple food that accounts for an important share of the daily protein, high grain protein contents help to improve the diet. In many farming systems, livestock is fed with dry or fresh maize stover. Selection for high NUtE, NHI, or low SNC will lead to varieties with low N concentrations in the stover or in the grain or in both. Thus, this breeding strategy may be inadvisable. In industrialized countries, maize grain is used mainly for animal feed and industrial purposes, where a high concentration of protein in maize is not the main goal due to the availability of inexpensive, high quality protein supplements. It is concluded that selecting for high NUtE alone is not a promising route to developing nutritious maize in developing countries.

6.3. Grain Mineral Contents

In the present study, there were significant genotypic differences in the concentrations of protein, P, K, Mg, Ca, Mn, Zn, and Cu in the grains. The varieties which differed most in the N and P concentrations had the same endosperm to germ dry weight ratio. Varietal differences in the elemental composition of maize kernels seem to be fairly stable under wide ranges of water and N supply. While the study showed that the concentrations of grain minerals are well buffered and remain stable even when the grain yield increases markedly as a result of water and N fertilizer applications, it must still be determined whether higher grain yields, as a result of breeding progress, tend to lower the levels of grain minerals and protein.

7. ZUSAMMENFASSUNG

In vielen tropischen Gebieten wird der Ertrag von Mais durch die Verfügbarkeit von Wasser und Stickstoff (N) limitiert. Unter den Bedingungen des thailändischen Tieflandes tritt Dürrestress insbesondere vor der Blüte auf, wohingegen die Wasserversorgung während der Blüte und der Kornfüllung zumeist ausreichend ist. Das Ziel der Versuche war, Informationen über die Effekte dieser bisher wenig untersuchten Form des Dürrestresses auf die Ertragsbildung verschiedener Maissorten bei unterschiedlicher N-Verfügbarkeit zu erhalten.

Material und Methoden

Die Versuche wurden auf den Feldern des National Corn and Sorghum Research Center, Farm Suwan, Pakchong, Thailand (Breite 14,5°N; 360 m.ü.M.), in den Trockenzeiten der Jahre 1995, 1996 und 1997 auf einem Lateritboden (klassifiziert als ustic, isohyperthermic, kaolinitic oxisol) durchgeführt. Es gab zwei Wasserregimes: In der gut bewässerten Variante wurden während der gesamten Vegetationsperiode wöchentlich etwa 50 mm Wasser durch Furchenbewässerung appliziert (= Kontrolle). In der Dürrestress-Variante wurden bis kurz vor der Blüte während zwei Perioden von vier Wochen jeweils kein Wasser verabreicht; danach wurde wie in der Kontrolle bewässert. Es gab drei N-Versorgungsstufen: 0, 80 und 80+80 kg N ha⁻¹, wobei die erste Gabe zur Saat und die zweite Gabe sechs Wochen nach der Saat verabreicht wurde. Zwei Hybridsorten (KTX2602 und DK888) und zwei offen abstäubende Sorten (Suwan 1 und La Posta Sequia) wurden angebaut. Der Versuch war als Spaltanlage mit sechs Wiederholungen angelegt, wobei die Wasserversorgung den 'main plot', die N-Stufe den 'sub-plot' und die Sorte den 'sub-subplot' bildeten. Es wurden unter anderem folgende Parameter in der vorliegenden Arbeit besprochen: Kornertrag und Ertragskomponenten, Ernteindex, N Trockenmasse in Korn und Gesamtpflanze, N-Ausnutzungseffizienz (Kornertrag pro N Trockenmasse in der Gesamtpflanze), N-Konzentration in Korn und Pflanze, N-Ernteindex und scheinbare Ausnutzung des Dünger N. Die N-Parameter wurden bezüglich ihrer Eignung als Züchtungskriterium beurteilt. Weiter wurden Sortenunterschiede und Wasser- und N-Effekte hinsichtlich der Mineralstoffkonzentrationen im Korn untersucht.

Ergebnisse und Diskussion

Wassereffekte: Gemittelt über alle Sorten, N-Stufen und Jahre reduzierte der Dürrestress den Kornertrag um 22%, wobei die Ertragseinbußen stark von Jahr zu Jahr schwankten (1995: 32%; 1996: 13%; 1997: 21%). Damit ist die negative Ertragswirkung von Vorblüte-Dürrestress offenbar

weitaus geringer als während der Blüte auftretender Wassermangel, welcher Ertragsreduktionen bis zu 90% verursachen kann. Der gesamte Biomassertrag wurde weitaus stärker durch den Dürrestress vermindert als der Kornertrag, so dass der Ernteindex von 44% (1995), 48% (1996) und 40% (1997) dürrebedingt auf über 50% stieg (1995: 54%; 1996: 52%; 1997: 46%). In allen Jahren reduzierte der Dürrestress signifikant die Anzahl Körnerreihen, die Anzahl Körner pro Reihe und das Tausendkorngewicht. Letzteres ist bemerkenswert, weil in der Wassermangelvariante bereits kurz vor der Blüte analog zur Kontrolle bewässert wurde und während der gesamten Kornfüllungsphase ausreichend Wasser zur Verfügung stand. Offensichtlich vermochten die Pflanzen in der Dürrestressvariante wegen der kleineren grünen Blattfläche weniger Assimilate zu bilden, womit zu Beginn der Kornfüllung wahrscheinlich weniger translozierbare Kohlenhydratreserven im Spross zur Verfügung standen. Der relativ geringe Einfluss der dürrebedingten Tausendkorngewicht-Reduktionen auf den Kornertrag zeigt, dass die Ertragseinbußen hauptsächlich aus einer verringerten Kornzahl pro Fläche resultierten. Die Kolbenzahl pro Pflanze wurde wenig von der Wasserversorgung beeinflusst; die mehrkolbige Sorte DK888 reagierte diesbezüglich nicht in allen Jahren gleich.

Stickstoff-Effekte: Bei ausreichender Wasserversorgung stieg der Kornertrag mit zunehmender N-Düngung an, während bei Dürrestress die Düngung von 160 kg N ha⁻¹ keinen Mehrertrag gegenüber der 80 kg N-Variante brachte. Dürrestress erhöhte einerseits die N-Konzentration in der Pflanze und den N-Ernteindex, und reduzierte andererseits die N Trockenmasse pro Fläche und die mittlere scheinbare Ausnutzung des Dünger-N in allen Jahren. Der Dürreeffekt auf die N-Ausnutzungseffizienz war inkonsistent über die Jahre. Mit steigenden N-Düngergaben nahmen der Kornertrag, die N Trockenmasse und die N Konzentration in der Pflanze zu; die N-Ausnutzungseffizienz, der N-Ernteindex und die mittlere scheinbare Ausnutzung des Dünger-N nahmen ab. Es gab in allen Jahren signifikante Sortenunterschiede in der N-Konzentration, der N-Ausnutzungseffizienz und dem N Ernteindex. Sporadische Interaktionen lassen jedoch keine einheitliche Schlussfolgerung bezüglich dem Wasser-, N- und Sorteneffekt auf die N-Ausnutzung zu. Angesichts des für Entwicklungsländer typischen Mangels an Proteinen in der menschlichen Ernährung und im Tierfutter ist es fragwürdig, auf eine erhöhte N-Ausnutzungseffizienz, und damit auf eine reduzierte N Konzentration in der Pflanze und im Korn, hin zu züchten.

Sorteneffekte: In zwei von drei Jahren wurden signifikante Wasserregime-Sorten-Interaktionen beim Kornertrag beobachtet. Der Hybrid KTX2602 war in allen Jahren stärker vom Dürrestress betroffen als Suwan 1, was möglicherweise auf eine kürzere vegetative Wachstumsphase von

KTX2602 zurückzuführen ist. Die ertragsstarke DK888 konnte im Jahr mit dem schwächsten Dürrestress ihr Ertragspotential trotz guter Wasser- und N-Versorgung nicht ausschöpfen und erntete praktisch gleich viel wie unter Dürrestress. Relativ hohe Temperaturen und geringe Sonnenstrahlung unmittelbar nach der Blüte scheinen für den tiefen Ertrag verantwortlich zu sein. La Posta Sequia wurde vom CIMMYT auf Toleranz gegenüber Dürrestress während der Blüte gezüchtet. Wegen der engen Beziehung zwischen dem Anthesis-Silking Intervall und Dürretoleranz selektiert das CIMMYT auf ein möglichst kurzes Anthesis-Silking Intervall, was in den Versuchen deutlich zum Ausdruck kam. Dennoch unterschied sich im Mittel der Jahre die Ertragsreaktion dieser Sorte auf Dürrestress nicht wesentlich von der der einheimischen Sorten. Wir schliessen daraus, dass das Anthesis-Silking Intervall als Züchtungsmerkmal nur dann relevant ist, wenn der Dürrestress während der Blüte auftritt.

Mineralstoffe im Korn: Die Konzentrationen im Korn von N, P, K, Mg, Ca, Mn, Zn und Cu wurden analysiert. In allen Jahren hatte der Dürrestress keinen Einfluss auf die Mineralstoffzusammensetzung. Hingegen reduzierte die N Düngergabe konsistent die Ca- und Zn-Konzentrationen, und erhöhte die Mn-Konzentration. Die ertragsstarke Sorte DK888 hatte in allen Jahren die tiefste Konzentrationen an N, P, Mg und Cu. Unregelmässige Interaktionen zwischen Sorte und Wasserregime, beziehungsweise N Düngung liessen keine Rangfolge der Sorten ausmachen. Das lässt die Schlussfolgerung zu, dass auf einem gegebenen Standort Sortenunterschiede in der Protein- und Mineralstoffkonzentration im Korn unter unterschiedlicher Wasser- und N-Versorgung relativ stabil sind. Es bleibt zu untersuchen, ob züchtungsbedingte Ertragssteigerungen zu tieferen Protein- und Mineralstoffgehalten führten.

REFERENCES

- Abrecht, D.G. and Carberry, P.S. (1993). The influence of water deficit prior to tassel initiation on maize growth, development and yield. *Field Crops Research* 31, 55-69.
- Adriaanse, F.G. and Human, J.J. (1993). Effect of time of application and nitrate: Ammonium ratio on maize grain yield, grain N concentration and soil mineral N concentration in a semi-arid region. *Field Crops Research* 34, 57-70.
- Ahmadi, M., Wiebold, W.J., and Beuerlein, J.E. (1993). Grain yield and mineral composition of corn as influenced by endosperm type and nitrogen. *Communications in Soil Science and Plant Analysis* 24, 2409-2426.
- Akintoye, H.A., Kling, J.G., and Lucas, E.O. (1999). N-use efficiency of single, double and synthetic maize lines grown at four N levels in three ecological zones of West Africa. *Field Crops Research* 60, 189-199.
- Alexander, D.E. (1988). Breeding special nutritional and industrial types. In "Corn and corn improvement" (Dudley, G.F.S.a.J.W., ed.), pp. 869-880. ASA, CSSA, SSSA., Madison, WI.
- Alfoldi, Z., Pinter, L., and Feil, B. (1994). Nitrogen, phosphorus and potassium concentrations in developing maize grains. *Journal of Agronomy and Crop Science* 172, 200-206.
- Anderson, E.L. (1987). Corn root growth and distribution as influenced by tillage and nitrogen fertilization. *Agronomy Journal* 79, 544-549.
- Anderson, E.L., Kamprath, E.J., and Moll, R.H. (1984). Nitrogen fertility effects on accumulation, remobilization, and partitioning of N and dry matter in corn genotypes differing in prolificacy. *Agronomy Journal* 76, 397-404.
- Anderson, E.L., Kamprath, E.J., and Moll, R.H. (1985). Prolificacy and N fertilizer effects on yield and N utilization in maize. *Crop Science* 25, 598-602.
- Andrade, F.H., Cirilo, A.G., and Echarte, L. (2000). Factors affecting kernel number in maize. In "Physiological bases for maize improvement" (Otegui, M.E. and Slafer, G.A., eds.), pp. 59-74.
- Arnold, F.B. and Bauman, L.F. (1976). Inheritance of and interrelationships among maize kernel traits and elemental contents. *Crop Science* 16, 439-440.
- Arnold, J.M., Bauman, L.F., and Aycock, H.S. (1977). Interrelations among protein, lysine, oil, certain mineral element concentrations, and physical kernel characteristics in two maize populations. *Crop Science* 17, 421-425.
- Asian Development Bank (2001). "Proposed technical assistance for the sixth agriculture and natural resources research at CGIAR centers."
- Attanandana, T. and Yost, R.S. (2003). A site-specific nutrient management approach for maize. *Better Crops International* 17, 3-7.
- Balko, L.G. and Russell, W.A. (1980). Response of maize inbred lines to N fertilizer. *Agronomy Journal* 72, 723-728.
- Banziger, M. (1992). Nitrogen efficiency of spring wheat genotypes (*Triticum aestivum* L.). Dissertation, ETHZ, Zürich.
- Banziger, M. (1999). Breeding for drought tolerance in tropical maize - conventional approaches and challenges to molecular approaches. In "Molecular approaches for the genetic improvement of cereals for stable production in water-limited environments" (Ribaut, J.-M., ed.), pp. 69-72. CIMMYT, Mexico.
- Banziger, M. and Long, J. (2000). The potential for increasing the iron and zinc density of maize through plant-breeding. *Food and Nutrition Bulletin* 21, 397-400.

- Banziger, M., Edmeades, G.O., and Lafitte, H.R. (1999). Selection for drought tolerance increases maize yields across a range of nitrogen levels. *Crop Science* 39, 1035-1040.
- Banziger, M., Edmeades, G.O., Beck, D., and Bellon, M. (2000). "Breeding for drought and nitrogen stress tolerance in maize: From theory to practice." CIMMYT.
- Bassetti, P. and Westgate, M.E. (1994). Floral asynchrony and kernel set in maize quantified by image analyses. *Agronomy Journal* 86, 933-703.
- Bauder, J.W., Hanks, R.J., and James, D.W. (1975). Crop production function determinations as influenced by irrigation and nitrogen fertilization using a continuous variable design. *Soil Science Society of America Proceedings* 39, 1187-1192.
- Beauchamp, E.G., Kannenberg, L.W., and Hunter, R.B. (1976). Nitrogen accumulation and translocation in corn genotypes following silking. *Agronomy Journal* 68, 418-422.
- Belhassen, E. (1997). "Drought tolerance in higher plants: Genetical, physiological and molecular biological analysis," Kluwer Academic Publishers, Dordrecht, NL.
- Bennett, J.M., Mutti, L.S.M., Rao, P.S.C., and Jones, J.W. (1989). Interactive effects of nitrogen and water stresses on biomass accumulation, nitrogen uptake, and seed yield of maize. *Field Crops Research* 19, 297-311.
- Bennett, W.F., Stanford, G., and Dumenil, L. (1953). Nitrogen, phosphorus and potassium content of the corn leaf and grain as related to nitrogen fertilization and yield. *Soil Science Society of America Proceedings* 17, 252-258.
- Bletsos, E.A. and Goulas, C.K. (1999). Mass selection for improvement of grain yield and protein in a maize population. *Crop Science* 39, 1302-1305.
- Blum, A. (1996). Crop responses to drought and the interpretation to adaptation. *Plant Growth Regulation* 20, 135-148.
- Blum, A. (1997). Constitutive traits affecting plant performance under stress. In "Developing Drought- and Low N-Tolerant Maize" (Edmeades, G.O., Banziger, M., Mickelson, H.R. and Peña-Valdivia, C.B., eds.), pp. 131-135. CIMMYT, El Batán, Mexico.
- Blum, A. and Johnson, J.W. (1992). Transfer of water from roots into dry soil and the effect on wheat water relations and growth. *Plant and Soil* 145, 141-149.
- Blum, A., Golan, G., Mayer, J., Sinmena, B., and Obilana, T. (1992). Comparative productivity and drought response of semi-tropical hybrids and open-pollinated varieties of sorghum. *Journal of Agricultural Science* 118, 29-36.
- Blumenthal, J.M., Lyon, D.J., and Stroup, W.W. (2003). Optimal plant population and nitrogen fertility for dryland corn in western nebraska. *Agronomy Journal* 95, 878-883.
- Bolaños, J. and Edmeades, G.O. (1993a). 8 cycles of selection for drought tolerance in lowland tropical maize. I. Responses in grain yield, biomass, and radiation utilization. *Field Crops Research* 31, 233-252.
- Bolaños, J. and Edmeades, G.O. (1993b). 8 cycles of selection for drought tolerance in lowland tropical maize. II. Responses in reproductive behavior. *Field Crops Research* 31, 253-268.
- Bolaños, J. and Edmeades, G.O. (1996). The importance of the anthesis-silking interval in breeding for drought tolerance in tropical maize. *Field Crops Research* 48, 65-80.
- Bolaños, J., Edmeades, G.O., and Martinez, L. (1993). 8 cycles of selection for drought tolerance in lowland tropical maize. III. Responses in drought-adaptive physiological and morphological traits. *Field Crops Research* 31, 269-286.
- Boyer, J.S. (1996). Advances in drought tolerance in plants. In "Advances in agronomy", Vol. 56. Academic Press, Inc.

- Boyle, M.G., Boyer, J.S., and Morgan, P.W. (1991). Stem infusion of liquid culture medium prevents reproductive failure of maize at low water potential. *Crop Science* 31, 1246-1252.
- Bruce, W.B., Edmeades, G.O., and Barker, T.C. (2002). Molecular and physiological approaches to maize improvement for drought tolerance. *Journal of Experimental Botany* 53, 13-25.
- Burman, R. and Pochop, L.O. (1994). "Evaporation, evapotranspiration and climatic data," Elsevier, NY.
- Burman, R.D., Painter, L.I., and Partridge, J.R. (1962). Irrigation and nitrogen fertilization of field corn in northwest Wyoming. *Agric Exp Stn Bull (Univ of Wyoming)* 389, 15.
- Byrne, P.F., Bolaños, J., Edmeades, G.O., and Eaton, D.L. (1995). Gains from selection under drought versus multilocation testing in related tropical maize populations. *Crop Science* 35, 63-69.
- Camp, K.-H. (1996). Transpiration efficiency of tropical maize (*Zea mays* L.). Dissertation, ETH, Zurich.
- Carberry, P.S., Muchow, R.C., and McCown, R.L. (1989). Testing the CERES-maize simulation model in a semi-arid tropical environment. *Field Crops Research* 20, 297-315.
- Carcova, J., Uribeharrea, M., Borrás, L., Otegui, M.E., and Westgate, M.E. (2000). Synchronous pollination within and between ears improves kernel set in maize. *Crop Science* 40, 1056-1061.
- Carter, W.W. and Ponoleit, C.G. (1973). Black layer maturity and filling period variation among inbred lines of corn (*Zea mays* L.). *Crop Science* 13, 436-439.
- Cassman, K.G., Dobermann, A., Walters, D.T., and Yang, H. (2003). Meeting cereal demand while protecting natural resources and improving environmental quality. *Annual Review of Environment and Resources* 28, 315-358.
- Ceccarelli, S., Valkoun, J., Erskine, W., Weigand, S., Miller, R., and Leur, J.A.G.v. (1992). Plant genetic resources and plant improvement as tools to develop sustainable agriculture. *Expl Agric* 28, 89-98.
- Central Intelligence Agency (2000). The world factbook. US Government.
- Cerrato, M.E. and Blackmer, A.M. (1990). Relationships between grain nitrogen concentration and nitrogen status of corn. *Agronomy Journal* 82, 744-749.
- Chevalier, P. and Schrader, L.E. (1977). Genotypic differences in nitrate absorption and partitioning of N among plant parts in maize. *Crop Science* 17, 897-901.
- CIMMYT (1994). In "Asian Regional Maize Research Planning and Coordination Meeting". CIMMYT, Farm Suwan, Nakorn Rachasima, Thailand.
- Claassen, M.M. and Shaw, R.H. (1970). Water deficits effects on corn. II. Grain components. *Agronomy Journal* 62, 652-655.
- Commuri, P.D. and Jones, R.J. (2001). High temperatures during endosperm cell division in maize: A genotypic comparison under in vitro and field conditions. *Crop Science* 41, 1122-1130.
- Costa, C., Dwyer, L.M., Stewart, D.W., and Smith, D.L. (2002). Nitrogen effects on grain yield and yield components of leafy and nonleafy maize genotypes. *Crop Science* 42, 1556-1563.
- Dampney, H.B. and Aspinall, D. (1976). Water deficit and inflorescence development in *Zea mays* L. *Annals of Botany* 40, 23-35.
- Denmead, O.T. and Shaw, R.H. (1960). The effects of soil moisture stress at different stages of growth on the development and yield of corn. *Agronomy Journal* 52, 272-274.
- Doorenbos, J. and Pruitt, W.O. (1977). "Guidelines for predicting crop water requirements," revised/Ed. FAO, Rome.
- Dowswell, C.R., Paliwal, R.L., and Cantrell, R.P. (1996). "Maize in the third world," Westview Press, Colorado, USA.
- Dudley, J.W. and Lambert, R.J. (1992). Ninety generations for oil and protein in maize. *Maydica* 37, 81-87.
- Dudley, J.W., Lambert, R.J., and Roche, I.A.D.L. (1977). Genetic analysis of crosses among corn strains divergently selected for percent oil and protein. *Crop Science* 17, 111-117.

- Durieux, R.P., Kamprath, E.J., and Moll, R.H. (1993). Yield contribution of apical and subapical ears in prolific and nonprolific corn. *Agronomy Journal* 85, 606-610.
- Durieux, R.P., Kamprath, E.J., Jackson, W.A., and Moll, R.H. (1994). Root distribution of corn: The effect of nitrogen fertilization. *Agronomy Journal* 86, 958-962.
- Duvick, D.N. and Cassman, K.G. (1999). Post-green revolution trends in yield potential of temperate maize in the North-central United States. *Crop Science* 39, 1622-1630.
- Earley, E.B., Miller, R.J., Reichert, G.L., Hagemann, R.H., and Seif, R.D. (1966). Effects of shade on maize production under field conditions. *Crop Science* 6, 1-7.
- Eberhard, D. (1977). Untersuchungen über den Einfluss von proteinreichen Inzuchtlinien auf die Ertragsgestaltung von Hybriden unter dem Aspekt der Körner- und Silonutzung von Mais (*Zea mays* L.). Dissertation, University of Hohenheim.
- Eck, H.E. (1984). Irrigated corn yield response to nitrogen and water. *Agronomy Journal* 76, 421-428.
- Eck, H.E. (1986). Effects of water deficits on yield, yield components, and water-use efficiency of irrigated corn. *Agronomy Journal* 78, 1035-1040.
- Edmeades, G.E. and Deutsch, J.A. (1994). "Stress tolerance breeding: Maize that resists insects, drought, low nitrogen, and acid soils," CIMMYT, Mexico, D.F.
- Edmeades, G.O., Banziger, M., and Ribaut, J.-M. (2000). Maize improvement for drought-limited environments. In "Physiological bases for maize improvement" (Otegui, M.E. and Slafer, G.A., eds.), pp. 75-111.
- Edmeades, G.O., Bolaños, J., Hernandez, M., and Bello, S. (1993). Causes for silk delay in a lowland tropical maize population. *Crop Science* 33, 1029-1035.
- Edmeades, G.O., Banziger, M., Chapman, S.C., Ribaut, J.-M., and Bolaños, J. (1995). "Recent advances in breeding for drought tolerance in maize," Paper presented at Sichuan Academy of Agricultural Sciences, Chengdu, P.R. China/Ed. CIMMYT, Mexico.
- Eghball, B. and Maranville, J.W. (1991). Interactive effects of water and nitrogen stresses on nitrogen utilization efficiency, leaf water status and yield of corn genotypes. *Communications in Soil Science and Plant Analysis* 22, 1367-1382.
- Eghball, B. and Maranville, J.W. (1993). Root development and nitrogen influx of corn genotypes grown under combined drought and nitrogen stresses. *Agronomy Journal* 85, 147-152.
- Elbchri, A., Putnam, D.H., and Schmitt, M. (1993). Nitrogen fertilizer and cultivar effects on yield and nitrogen-use efficiency of grain amaranth. *Agronomy Journal* 85, 120-128.
- Evans, L.T. (1993). "Crop evolution, adaption, and yield," Cambridge University Press.
- Feil, B. (1994). Effects of cultivar and nitrogen on the levels of protein and mineral elements in the grains of wheat, triticale, and maize (not published). Professorial Dissertation, ETH, Zürich.
- Feil, B. (1997). The inverse yield-protein relationship in cereals: Possibilities and limitations for genetically improving the grain protein yield. *Trends in Agronomy* 1, 103-119.
- Feil, B. (1998). Physiologische und pflanzenbauliche Aspekte der inversen Beziehung zwischen Ertrag und Proteinkonzentration bei Getreidesorten: Eine Übersicht. *Pflanzenbauwissenschaften* 2, 37-46.
- Feil, B. (2001). Phytic acid. *Journal of New Seeds* 3, 1-35.
- Feil, B. and Stamp, P. (1993). Sustainable agriculture and product quality: A case study for selected crops. *Food Reviews International* 9, 361-388.
- Feil, B. and Fossati, D. (1997). Phytic acid in triticale grains as affected by cultivar and environment. *Crop Science* 37, 916-921.
- Feil, B., Thiraporn, R., and Stamp, P. (1992a). Can maize cultivars with low mineral nutrient concentrations in the grains help to reduce the need for fertilizers in third-world countries. *Plant and Soil* 146, 227-231.

- Feil, B., Thiraporn, R., and Lafitte, H.R. (1993). Accumulation of nitrogen and phosphorus in the grain of tropical maize cultivars. *Maydica* 38, 291-300.
- Feil, B., Thiraporn, R., Geisler, G., and Stamp, P. (1990). Genotype variation in grain nutrient concentration in tropical maize grown during a rainy and a dry season. *Agronomie* 10, 717-725.
- Feil, B., Thiraporn, R., Geisler, G., and Stamp, P. (1992b). Yield, development and nutrient efficiency of temperate and tropical maize germplasm in the tropical lowlands. I. Yield and development. *Maydica* 37, 191-197.
- Fischer, K.S. and Palmer, A.F.E. (1984). Tropical maize. In "The physiology of tropical field crops" (Goldsworthy, P.R. and Fisher, N.M., eds.), pp. 213-248. John Wiley & Sons Ltd., Chichester, UK.
- Food and Agriculture Organization (2003). FAOSTAT, database collections.
- Francis, D.D., Schepers, J.S., and Vigil, M.F. (1993). Post-anthesis nitrogen loss from corn. *Agronomy Journal* 85, 659-663.
- Girardin, P., Tollenaar, M., Deltour, A., and Muldoon, J. (1987). Temporary N starvation in maize (*Zea mays* L.): Effects on development, dry matter accumulation and grain yield. *Agronomie* 7, 289-296.
- Graham, R., Senadhira, D., Beebe, S., Iglesias, C., and Monasterio, I. (1999). Breeding for micronutrient density in edible portions of staple food crops: Conventional approaches. *Field Crops Research* 60, 57-80.
- Grant, R.F., Jackson, B.S., Kiniry, J.R., and Arkin, G.F. (1989). Water deficit timing effects on yield components in maize. *Agronomy Journal* 81, 61-65.
- Gupta, D., Kovacs, I., and Gaspar, L. (1975). Protein quality and their relationships to yield and yield components of *opaque-2* and analogous normal maize hybrids and inbred lines. *Theoretical and Applied Genetics* 45, 341-348.
- Gutschik, V.P. (1981). Evolved strategies in nitrogen acquisition by plants. *American Naturalist* 118, 607-637.
- Hall, A.J., Lemcoff, J.H., and Trapani, N. (1981). Water stress before and during flowering in maize and its effects on yield, its components, and their determinants. *Maydica* 26, 19-38.
- Hall, A.J., Vilella, F., Trapani, N., and Chimenti, C. (1982). The effects of water stress and genotype on the dynamics of pollen-shedding and silking in maize. *Field Crops Research* 5, 349-363.
- Hancock, J.D., Pco, E.R., Lewis, A.J., Kniep, K.R., and Mason, S.C. (1988). Effects of irrigation and nitrogen fertilization of normal and high lysine corn on protein utilization by the growing rate. *Nutrition Reports International* 38, 413-422.
- Hanway, J.J. (1962). Corn growth and composition in relation to soil fertility: II. Uptake of N, P, and K and their distribution in different plant parts during the growing season. *Agronomy Journal* 54, 217-222.
- Hanway, J.J. and Ritchie, S.W. (1971). How a corn plant develops. *Iowa State University of Science and Technology* Special Report No 48.
- Harder, H.J., Carlson, R.E., and Shaw, R.H. (1982). Yield, yield components, and nutrient content of corn grain as influenced by post-silking moisture stress. *Agronomy Journal* 74, 275-278.
- Harrington, L.S., Whangthongtham, S., Witawat, P., Meesawat, R., and Suriyo, S. (1991). Beyond on-farm trials: The role of policy in explaining non-adoption of fertilizer on maize in Thailand. In "11th Annual AFSRE Symposium", pp. 1-34. AFSRE, Michigan State University, East Lansing.
- Harris, R.E., Moll, R.H., and Stuber, C.W. (1976). Control and inheritance of prolificacy in maize. *Crop Science* 16, 843-850.

- Hay, R.K.M. and Gilbert, R.A. (2001). Variation in the harvest index of tropical maize: Evaluation of recent evidence from Mexico and Malawi. *Annals of Applied Biology* 138, 103-109.
- Heisey, P.W. and Edmeades, G.O. (1999). "World maize facts and trends 1997/98." CIMMYT.
- Herrero, M.P. and Johnson, R.R. (1981). Drought stress and its effects on maize reproductive systems. *Crop Science* 21, 105-110.
- Hirel, B., Bertin, P., Quillere, I., Bourdoncle, W., Attagnant, C., Dellay, C., Gouy, A., Cadiou, S., Retalliau, C., Falque, M., and Gallais, A. (2001). Towards a better understanding of the genetic and physiological basis for nitrogen use efficiency in maize. *Plant Physiology* 125, 1258-1270.
- Howell, T.A., Tolck, J.A., Schneider, A.D., and Evett, S.R. (1998). Evapotranspiration, yield, and water use efficiency of corn hybrids differing in maturity. *Agronomy Journal* 90, 3-9.
- Jensen, S.D. and Cavalieri, A.J. (1983). Drought tolerance in US maize. *Agricultural Water Management* 7, 223-236.
- Jurgens, S.K., Johnson, R.R., and Boyer, J.S. (1978). Dry matter production and translocation in maize subjected to drought during grain filling. *Agronomy Journal* 70, 678-682.
- Karlen, D.L., Flannery, R.L., and Sadler, E.J. (1988). Aerial accumulation and partitioning of nutrients by corn. *Agronomy Journal* 80, 332-342.
- Kiniry, J.R. and Ritchie, J.T. (1985). Shade-sensitive interval of kernel number of maize. *Agronomy Journal* 77, 711-715.
- Kitbamroong, C. and Chantachume, Y. (1992). Corn improvement for drought tolerance. In "Adaptation of food crops to temperature and water stress" (Kuo, C.G., ed.), Vol. 34, pp. 354-359. AVRDC, Taiwan.
- Klepper, B. (1991). Crop root system response to irrigation. *Irrigation Science* 12, 105-108.
- Kling, J.G., Oikeh, S.O., Akintoye, H.A., Heuberger, H.T., and Horst, W.J. (1996). Potential for developing nitrogen use efficient maize for low input agricultural systems in the moist savannas of Africa. In "Developing Drought- and Low N-Tolerant Maize" (Edmeades, G.O., Banziger, M., Mickelson, H.R. and Peña-Valdivia, C.B., eds.), pp. 490-501. CIMMYT, El Batán, Mexico.
- Kniep, K.R. and Mason, S.C. (1989). Kernel breakage and density of normal and *opaque-2* maize grain as influenced by irrigation and nitrogen. *Crop Science* 29, 158-163.
- Kniep, K.R. and Mason, S.C. (1991). Lysine and protein content of normal and *opaque-2* maize grain as influenced by irrigation and nitrogen. *Crop Science* 31, 177-181.
- Lafitte, H.R. and Edmeades, G.O. (1988). An update on selection under stress: Selection criteria. In "Second Eastern, Central and Southern African Regional Maize Workshop" (Gclaw, B., ed.), pp. 309-331. The College Press, Harare, Zimbabwe.
- Lafitte, H.R. and Edmeades, G.O. (1994). Improvement for tolerance to low soil nitrogen in tropical maize I. Selection criteria. *Field Crops Res* 39, 1-14.
- Lafitte, H.R., Edmeades, G.O., and Taba, S. (1997). Adaptive strategies identified among tropical maize landraces for nitrogen-limited environments. *Field Crops Research* 49, 187-204.
- Landbeck, M.V. (1995). Untersuchungen zur genetischen Verbesserung der Anbaueignung von Körnermais unter Produktionsbedingungen mit verringerter Stickstoffversorgung. Dissertation, Universität Hohenheim, Stuttgart/D.
- Lantzsch, H.-J., Hillenbrand, S., Scheuermann, S.E., and Menke, K.H. (1991). Comparative study of phosphorus utilization from wheat, barley and corn diets by young rats and pigs. *Journal of Animal Physiology and Animal Nutrition* 67, 123-132.
- Lemcoff, J.H. and Loomis, R.S. (1986). Nitrogen influences on yield determination in maize. *Crop Science* 26, 1017-1022.

- Leon, C. and Paroda, R.S. (1993). "Strategies for increasing maize production in the Asian-Pacific region," RAPA publication: 1993/25/Ed. FAO, Bangkok.
- Levitt, J. (1980). "Stress terminology," Wiley, New York.
- Littell, R.C., Miliken, G.A., Stroup, W.W., and Wolfinger, R.D. (1996). "SAS system for mixed models," SAS Institute Inc., Cary, NC.
- Lorens, G.F., Bennett, J.M., and Loggale, L.B. (1987a). Differences in drought resistance between two corn hybrids. I. Water relations and root length density. *Agronomy Journal* 79, 802-807.
- Lorens, G.F., Bennett, J.M., and Loggale, L.B. (1987b). Differences in drought resistance between two corn hybrids. II. Component analyses and growth rates. *Agronomy Journal* 79, 808-813.
- Lott, J.N.A., Ockenden, I., Raboy, V., and Batten, G.D. (2000). Phytic acid and phosphorus in crop seeds and fruits: A global estimate. *Seed Science Research* 10, 11-33.
- Machado, A.T. and Fernandez, M.S. (2001). Participatory maize breeding for low nitrogen tolerance. *Euphytica* 122, 567-573.
- Magson, J. (1996). Toward drought tolerant maize in South Africa. In "Developing Drought- and Low N-Tolerant Maize" (Edmeades, G.O., Banziger, M., Mickelson, H.R. and Peña-Valdivia, C.B., eds.), pp. 455-459. CIMMYT, El Batán, Mexico.
- Mambelli, S. and Stetter, T.L. (1998). Inhibition of maize endosperm cell division and endoreduplication by exogenously applied abscisic acid. *Physiologia Plantarum* 1998, 266-272.
- Manupeerapan, T., Chantachume, Y., Grudloyma, P., Thong-Chuay, S., and Noradechanon, S. (1997). Maize breeding for drought tolerance in Thailand. In "Developing Drought- and Low N-Tolerant Maize" (Edmeades, G.O., Banziger, M., Mickelson, H.R. and Peña-Valdivia, C.B., eds.), pp. 450-454. CIMMYT, El Batán, Mexico.
- Matthews, R.B., Azam-Ali, S.N., and Peacock, J.M. (1990). Response of four sorghum lines to mid-season drought. I. Growth, water use and yield. *Field Crops Research* 25, 279-296.
- Maziya-Dixon, B., Kling, J.G., Menkir, A., and Dixon, A. (2000). Genetic variation in total carotene, iron, and zinc contents of maize and cassava genotypes. *Food and Nutrition Bulletin* 21, 419-422.
- Meisinger, J.J., Bandel, V.A., Stanford, G., and Legg, J.O. (1985). Nitrogen utilization of corn under minimal tillage and moldboard plow tillage I. Four-year results using labeled N fertilizer on an atlantic coastal plain soil. *Agronomy Journal* 77, 602-611.
- Miller, D.F. (1958). Composition of cereal grains and forages. Committee on feed composition. *Board on Agriculture Publication* 585.
- Moll, R.H., Kamprath, E.J., and Jackson, W.A. (1982). Analysis and interpretation of factors which contribute to efficiency of nitrogen utilization. *Agronomy Journal* 74, 562-564.
- Moll, R.H., Kamprath, E.J., and Jackson, W.A. (1987). Development of nitrogen-efficient prolific hybrids of maize. *Crop Science* 27, 181-186.
- Motto, M. and Moll, R.H. (1983). Prolificacy in maize: A review. *Maydica* 28, 53-76.
- Muchow, R.C. (1988a). Effect of nitrogen supply on the comparative productivity of maize and sorghum in a semi-arid tropical environment I. Leaf growth and leaf nitrogen. *Field Crops Research* 18, 1-16.
- Muchow, R.C. (1988b). Effect of nitrogen supply on the comparative productivity of maize and sorghum in a semi-arid tropical environment III. Grain yield and nitrogen accumulation. *Field Crops Research* 18, 31-43.
- Muchow, R.C. (1989). Comparative productivity of maize, sorghum and pearl millet in a semi-arid tropical environment II. Effect of water deficits. *Field Crops Research* 20, 207-219.
- Muchow, R.C. (1990). Effect of nitrogen on partitioning and yield in grain sorghum under differing environmental conditions in the semi-arid tropics. *Field Crops Research* 25, 265-278.

- Muchow, R.C. (2000). Improving maize grain yield potential in the tropics. In "Physiological bases for maize improvement" (Otegui, M.E. and Slafer, G.A., eds.), pp. 47-58. Food Product Press.
- Muchow, R.C. and Davis, R. (1988). Effect of nitrogen supply on the comparative productivity of maize and sorghum in a semi-arid tropical environment II. Radiation interception and biomass accumulation. *Field Crops Research* 18, 17-30.
- Murphy, J. and Riley, J.P. (1962). A modified single solution method for the determination of phosphate in natural waters. *Analytical Chemistry Acta* 27, 31-36.
- Muruli, B.I. and Paulsen, G.M. (1981). Improvement of nitrogen use efficiency and its relationship to other traits in maize. *Maydica* 26, 63-73.
- National Identity Office, R.T.G. (1997). "The agriculture and mining sectors (in Thailand)," Mahidol University.
- Neidhart, B. (1994). Morphological and physiological responses to tropical maize (*Zea mays* L.) to pre-anthesis drought. Dissertation, ETH Zurich.
- Nesmith, D.S. and Ritchie, J.T. (1992). Short-term and long-term responses of corn to a pre-anthesis soil water deficit. *Agronomy Journal* 84, 107-113.
- Nielson, D.C. and Hinkle, S.E. (1996). Field evaluation of basal crop coefficients for corn based on growing degree days, growth stage, or time. *Transactions of the ASAE* 39, 97-103.
- Nilson, E.T. and Orcutt, D.M. (1996). Water limitation. In "The physiology of plants under stress" (Nilson, E.T. and Orcutt, D.M., eds.). Wiley & Sons, Inc., New York.
- O'Dell, B.L., A.R. de Boland, and Koirtzohann, S.R. (1972). Distribution of phytate and nutritionally important elements among the morphological components of cereal grains. *Journal of Agricultural Food Chemistry* 20, 718-721.
- Oikeh, S.O., Kling, J.G., and Okoruwa, A.E. (1998). Nitrogen fertilizer management effects on maize grain quality in the West African moist savanna. *Crop Science* 38, 1056-1061.
- Oikeh, S.O., Kling, J.G., Horst, W.J., Chude, V.O., and Carsky, R.J. (1999). Growth and distribution of maize roots under nitrogen fertilization in plinthite soil. *Field Crops Research* 62, 1-13.
- Olsen, M.S., Krone, T.L., and Phillips, R.L. (2003). Bsss53 as a donor source for increased whole-kernel methionine in maize: Selection and evaluation of high-methionine inbreds and hybrids. *Crop Science* 43, 1634-1642.
- Olsen, S.R. and Sommers, L.E. (1982). Phosphorus. In "Methods of soil analysis part 2 chemical and microbiological properties" (Page, A.L., ed.), pp. 403-430. ASA-SSSA, Madison, WI.
- Pan, W.L., Camberato, J.J., Moll, R.H., Kamprath, E.J., and Jackson, W.A. (1995). Altering source-sink relationships in prolific maize hybrids: Consequences for nitrogen uptake and remobilization. *Crop Science* 35, 836-845.
- Pandey, R.K., Maranville, J.W., and Admou, A. (2000). Deficit irrigation and nitrogen effects on maize in a Sahelian environment: I. Grain yield and yield components. *Agricultural Water Management* 46, 1-13.
- Passioura, J.B. (1996). Drought and drought tolerance. *Plant Growth Regulation* 20, 79-83.
- Pearson, C.J. and Jacobs, B.C. (1987). Yield components and nitrogen partitioning of maize in response to nitrogen before and after anthesis. *Australian Journal of Agricultural Research* 38, 1001-1009.
- Peters, C.J., Fick, G.W., and Wilkins, J.L. (2003). Cultivating better nutrition: Can the food pyramid help translate dietary recommendations into agricultural goals? *Agronomy Journal* 95, 1424-1431.
- Petrie, C.L. and Hall, A.E. (1992). Water relations in cowpea and pearl millet under soil water deficits. II. Water use and root distribution. *Australian Journal of Plant Physiology* 19, 591-600.

- Pierre, W.H., Dumcnil, L., Jolley, V.D., Webb, J.R., and Schrader, W.D. (1977). Relationship between corn yield, expressed as a percentage of maximum, and the N percentage in the grain I. Various N-rate experiments. *Agronomy Journal* 69, 215-220.
- Pictz, R.I., Peterson, J.R., Lue-Hing, C., and Welch, L.F. (1978). Variability in the concentration of twelve elements in corn grain. *Journal of Environmental Quality* 7, 106-110.
- Pixley, K.V. and Bjarnason, M.S. (1993). Combining ability for yield and protein quality among modified endosperm *opaque-2* tropical maize inbreds. *Crop Science* 33, 1229-1234.
- Pixley, K.V. and Bjarnason, M.S. (2002). Stability of grain yield, endosperm modification, and protein quality of hybrid and open-pollinated quality protein maize (QPM) cultivars. *Crop Science* 42, 1882-1890.
- Pollmer, W.G., Eberhard, D., Klein, D., and Dhillon, B.S. (1979). Genetic control of nitrogen uptake and translocation in maize. *Crop Science* 19, 83-86.
- Presterl, T., Groh, S., Landbeck, M., Seitz, G., Schmidt, W., and Geiger, H.H. (2002). Nitrogen uptake and utilization efficiency of european maize hybrids developed under conditions of low and high nitrogen input. *Plant Breeding* 121, 480-486.
- Prine, G.M. (1971). A critical period for ear development in maize. *Crop Science* 11, 782-786.
- Raboy, V., Below, F.E., and Dickinson, D.B. (1989). Alteration of maize kernel phytic acid levels by recurrent selection for protein and oil. *Journal of Heredity* 80, 311-315.
- Richards, R.A. (1989). "Breeding for drought resistance - physiological approaches," CAB International, UK.
- Richards, R.A. (1996). Defining selection criteria to improve yield under drought. *Plant Growth Regulation* 20, 157-166.
- Richards, R.A., Lopez-Castañeda, C., Gomez-Macpherson, H., and Condon, A.G. (1993). Improving the efficiency of water use by plant breeding and molecular biology. *Irrigation Science* 14, 93-104.
- Rosenberg, N.J., Blad, B.L., and Verma, S.B. (1983). "Microclimate; the biological environment," 2nd/Ed. John Wiley & Sons, NY.
- Sallah, P.Y.K., Ehlke, N.J., and Geadelmann, J.L. (1996). Selection for response to low nitrogen in the la posta maize population. In "Developing Drought- and Low N-Tolerant Maize" (Edmeades, G.O., Banziger, M., Mickelson, H.R. and Peña-Valdivia, C.B., eds.), pp. 503-507. CIMMYT, El Batán, Mexico.
- Sarquis, J.I., Gonzalez, H., and Dunlap, J.R. (1998). Yield response of two cycles of selection from a semiprofliferous early maize (*Zea mays* L.) population to plant density, sucrose infusion and pollination control. *Field Crops Research* 55, 109-116.
- SAS Institute Inc. (1997). "SAS/STATc user's guide," 6.12/Ed., Cary, NC.
- Sattelmacher, B., Horst, W.J., and Becker, H.C. (1994). Factors that contribute to genetic variation for nutrient efficiency of crop plants. *Zeitschrift für Pflanzenernährung und Bodenkunde* 157, 215-224.
- Scharf, P.C., Wiebold, W.J., and Lory, J.A. (2002). Corn yield response to nitrogen fertilizer timing and deficiency level. *Agronomy Journal* 94, 435-441.
- Schindler, F.V. and Knighton, R.E. (1999). Fate of fertilizer nitrogen applied to corn as estimated by the isotopic and difference methods. *Soil Science Society of America Journal* 63, 1734-1740.
- Schnug, E. and Finck, A. (1980). Einfluss unterschiedlicher Stickstoffdüngerformen auf die Mobilisierung von Spurennährstoffen. *Landwirtschaftliche Forschung, Sonderheft* 37, 243-253.
- Schoper, J.B., Lambert, R.J., and Vasilas, B.L. (1986). Maize pollen viability and ear receptivity under water and high temperature stress. *Crop Science* 26, 1029-1033.

- Schreiber, H.A., Stanberry, C.O., and Tucker, H. (1962). Irrigation and nitrogen effects on sweet corn row numbers at various growth stages. *Science* 135, 1135-1136.
- Schussler, J.R. and Westgate, M.E. (1995). Assimilate flux determines kernel set at low water potential in maize. *Crop Science* 35, 1074-1080.
- Sharp, R.E. and Davies, W.J. (1989). Regulation of growth and development of plants growing with a restricted supply of water. *Plants under Stress*, 71-93.
- Sinclair, T.R. and Vadez, V. (2002). Physiological traits for crop yield improvement in low N and P environments. *Plant and Soil* 245, 1-15.
- Sinclair, T.R., Bennett, J.M., and Muchow, R.C. (1990). Relative sensitivity of grain yield and biomass accumulation to drought in field-grown maize. *Crop Science* 30, 690-693.
- Siri, B. (1993). Influence of drought stress on seedling growth and leaf anatomy as related to yield components and grain yield of tropical maize cultivars. Ph.D. thesis, Christian-Albrechts-University of Kiel.
- Soil Science Department (1994). "Exercise and handbook for plant and soil analysis," Faculty of Agriculture, Kasetsart University, Bangkok, Thailand.
- Stanberry, C.O., Schreiber, H.A., Lowrey, M., and Jenson, C.L. (1963). Sweet corn production as affected by moisture and nitrogen variables. *Agronomy Journal* 55, 159-161.
- Thiraporn, R., Geisler, G., and Stamp, P. (1983). Yield and relationship among yield components and N- and P-related traits in maize genotypes under tropical conditions. *Journal of Agronomy and Crop Science* 152, 460-468.
- Thiraporn, R., Feil, B., and Stamp, P. (1992). Effect of nitrogen fertilization on grain yield and accumulation of nitrogen, phosphorus and potassium in the grains of tropical maize. *Journal of Agronomy and Crop Science* 169, 9-16.
- Thomison, P.R. and Jordan, D.M. (1995). Plant population effects on corn hybrids differing in ear growth habit and prolificacy. *Journal of Production Agriculture* 8, 394-400.
- Tollenaar, M. and Wu, J. (1999). Yield improvement in temperate maize is attributable to greater stress tolerance. *Crop Science* 39, 1597-1604.
- Tollenaar, M. and Dwyer, L.M. (1999). Physiology of maize. In "Crop yield; physiology and processes" (Smith, D.L. and Hamel, C., eds.), pp. 169-204. Springer, Berlin Heidelberg, DE.
- Tsai, C.Y., Dweikat, I., Huber, D.M., and Warren, H.L. (1992). Interrelationship of nitrogen nutrition with maize (*Zea mays* L.) grain yield, nitrogen use efficiency and grain quality. *Journal of the Science of Food and Agriculture* 58, 1-8.
- Turner, N.C. (2002). Drought resistance: A comparison of two research frameworks. In "Management of agricultural drought : Agronomic and genetic options" (Saxena, N.P., ed.), pp. 89-102. Science Publishers Inc., NH, USA.
- Uhart, S.A. and Andrade, F.H. (1995). Nitrogen deficiency in maize: I. Effects on crop growth, development, dry matter partitioning, and kernel set. *Crop Science* 35, 1376-1383.
- Van Campen, D.R. and Glahn, R.P. (1999). Micronutrient bioavailability techniques: Accuracy, problems and limitations. *Field Crops Research* 60, 93-113.
- Van Dijk, W. and Brouwer, G. (1998). Nitrogen recovery and dry matter production of silage maize (*Zea mays* L.) as affected by surface band application of mineral nitrogen fertilizer. *Netherlands Journal of Agricultural Science* 46, 139-155.
- Vyn, T.J. and Tollenaar, M. (1998). Changes in chemical and physical quality parameters of maize during three decades of yield improvement. *Field Crops Research* 59, 135-140.
- Watson, S.A. (1987). Structure and composition. In "Corn: Chemistry and technology" (Watson, S.A. and Ramstad, P.E., eds.), pp. 53-82. American Association of Cereal Chemists, St. Paul, MI, USA.

- Weerathaworn, P., Soldati, A., and Stamp, P. (1992a). Anatomy of seedling roots of tropical maize (*Zea mays* L.) cultivars at low water supply. *Journal of Experimental Botany* 43, 1015-1021.
- Weerathaworn, P., Thiraporn, R., Soldati, A., and Stamp, P. (1992b). Yield and agronomic characters of tropical maize (*Zea mays* L.) cultivars under different irrigation regimes. *Journal of Agronomy and Crop Science* 168, 326-336.
- Weiland, R.T. and Ta, C.T. (1992). Allocation and retranslocation of ^{15}N by maize (*Zea mays* L.) hybrids under field conditions of low and high fertility. *Australian Journal of Plant Physiology* 19, 77-88.
- Welch, R.M. and Graham, R.D. (2004). Breeding for micronutrients in staple food crops from a human nutrition perspective. *Journal of Experimental Botany* 55, 353-364.
- Westgate, M.E. and Boyer, J.S. (1986). Reproduction at low silk and pollen water potentials in maize. *Crop Science* 26, 951-956.
- Westgate, M.E. and Thomson Grant, D.L. (1989). Water deficits and reproduction in maize. Response of the reproductive tissue to water deficits at anthesis and mid-grain fill. *Plant Physiology* 91, 862-867.
- Wetselaar, R. and Farquhar, G.D. (1980). Nitrogen losses from tops of plants. *Advances in Agronomy* 33, 263-302.
- Wyss, C.S., Czyzewicz, J.R., and Below, F.E. (1991). Source-sink control composition in maize strains divergently selected for protein concentration. *Crop Science* 31, 761-766.
- Zink, F. and Michael, G. (1985). The effect of reduced number of kernels and of leaves per plant on the nitrogen storage characteristics of the kernels of two maize hybrids with different grain-N-content. *Journal of Agronomy and Crop Science* 154, 203-212.

APPENDIX

Table A1: Duration, evapotranspiration crop (ET_{crop}), growing degree days (GDD) and mean air temperature (temp.) of different growing periods in 1995, 1996, and 1997

Growing period	Duration	ET_{crop}	$ET_{crop} d^{-1}$	GDD	GDD d^{-1}	Mean air temp.
	day	mm	mm d^{-1}	$^{\circ}Cd$	$^{\circ}Cd d^{-1}$	$^{\circ}C$
<u>1995</u>						
Whole season	115	331.6	2.9	1571.8	13.7	24.9
pre-anthesis	62	175.4	2.8	774.5	12.5	23.1
1 st stress period	20 [†]	41.9	2.1	261	13.1	23.4
2 nd stress period	17	61.7	3.6	226.3	13.3	23.7
<u>1996</u>						
Whole season	124	334.9	2.7	1632.5	13.2	23.9
pre-anthesis	62	154.4	2.5	723.8	11.7	21.8
1 st stress period	16	32.3	2.0	208.3	13.0	23.0
2 nd stress period	20	66.2	3.3	236.3	11.8	22.1
<u>1997</u>						
Whole season	121	314.5	2.6	1623.8	13.4	24.2
pre-anthesis	65	163.3	2.5	808.5	12.4	22.6
1 st stress period	22	46.4	2.1	258.8	11.8	21.8
2 nd stress period	14	38.6	2.8	194.8	13.9	24.5

[†] Days with effective drought stress

Table A2: Main effects of water regime, rate of N application, and variety on days from plant emergence to 50% silking and anthesis-silking interval (ASI) in 1995, 1996, and 1997; results of *F*-tests for the effects of main factors and interactions.

	Days to 50% silking					ASI (days)		
	1995	1996	1997	1995	1996	1997	1996	1997
Grand mean	63.4	63.3	67.5	0.7	0.9	0.4		
<u>Water regime</u>								
Well-watered	61.2 b ¹	62.2 b	65.2 b	0 b	0 b	-0.1 b		
Drought-stressed	65.6 a	64.4 a	69.8 a	1.5 a	1.8 a	0.7 a		
<u>N rate</u>								
0 kg N ha ⁻¹	65.1 a	63.9 a	69.6 b	0.9	0.7	0.6 a		
80 kg N ha ⁻¹	62.8 b	63.4 b	66.4 a	0.7	0.8	0.1 b		
160 kg N ha ⁻¹	62.3 b	62.7 b	66.4 a	0.5	1.1	0.1 b		
<u>Variety</u>								
Suwan 1	64.3 a	65.1 a	67.3 c	0.3 b	1.6 a	0.2 b		
La Posta Sequia	64.3 a	63.7 b	69.1 b	-0.6 c	-0.9 b	-1.1 c		
KTX2602	60.7 b	59.2 c	63.3 d	2.8 a	1.4 a	1.2 a		
DK888	64.3 a	65.4 a	70.2 a	0.5 b	1.4 a	0.6 b		
<u>F-tests</u>								
Water regime (W)	**	***	***	***	***	***	***	**
N rate (N)	***	**	***	ns	ns	*	ns	*
Variety (Var)	***	***	***	***	***	***	***	***
W x N	ns	ns	*	*	ns	ns	ns	ns
W x Var	ns	ns	**	***	*	*	*	*
N x Var	ns	ns	ns	ns	ns	ns	ns	ns
W x N x Var	**	ns	ns	*	ns	ns	ns	ns

*, **, *** significant at P=0.05, 0.01, 0.001, respectively. ns not significant.

¹ Means not followed by the same letter within a column are significantly different according to Fisher's protected LSD test at P=0.05.

Table A.3: Main effects[†] of variety, water regime, and rate of N application on grain yield and concentrations of grain N and minerals in 1995.

	Grain yield		g kg ⁻¹				µg kg ⁻¹			
	Mg ha ⁻¹		N	P	K	Mg	Ca	Zn	Mn	Cu
Grand mean	5.42		14.6	3.29	3.93	1.13	137	25.0	6.45	2.21
<u>Water regime</u>										
Drought-stressed	4.37 b [†]		14.4	3.21	3.94	1.11	138	24.1	6.34	2.27
Well-watered	6.46 a		14.8	3.37	3.93	1.14	135	25.9	6.56	2.15
F-test	***		ns	ns	ns	ns	ns	ns	ns	ns
<u>Rate of N fertilizer</u>										
0 kg ha ⁻¹	4.27 b		13.8 c	3.29	3.95	1.10	147 a	26.2 a	6.17	2.15
80 kg ha ⁻¹	5.81 a		14.6 b	3.34	3.94	1.14	131 b	24.9 ab	6.49	2.24
160 kg ha ⁻¹	6.18 a		15.4 a	3.24	3.91	1.14	132 b	24.0 b	6.68	2.25
F-test	***		***	ns	ns	ns	***	*	ns	ns
<u>Variety</u>										
Suwan I	4.90 bc		14.7 b	3.24 b	3.96	1.06 b	142 a	26.4 a	6.18 b	2.44 a
La Posta Sequia	5.39 b		14.6 b	3.19 b	3.96	1.11 b	129 b	23.6 b	5.91 b	2.11 bc
KTX2602	4.74 c		15.6 a	3.68 a	4.09	1.26 a	146 a	26.0 a	7.64 a	2.34 ab
DK888	6.64 a		13.6 c	3.06 b	3.74	1.06 b	129 b	24.1 b	6.05 b	1.96 c
F-test	***		***	***	ns	***	***	**	***	***

*, ***, significant at P=0.05 and 0.01, respectively. ns not significant.

[†] The effect of the water regime x N rate interaction on grain yield was significant (see Table 3); the effects of the remaining two-way and all three-way interactions were not significant.

[‡] Means not followed by the same letter within a column are significantly different.

Table A.4: Main effects[†] of variety, water regime, and rate of N application on grain yield and concentrations of grain N and minerals in 1996.

	Grain yield		g kg ⁻¹							µg kg ⁻¹		
	Mg ha ⁻¹		N	P	K	Mg	Ca	Zn	Mn	Cu		
Grand mean	6.59		13.6	3.16	3.71	1.12	82.0	23.1	6.92	2.36		
<u>Water regime</u>												
Drought-stressed	6.15 b [‡]		13.9 a	3.21	3.72	1.13	84.0	23.5	7.11	2.37		
Well-watered	7.03 a		13.3 b	3.11	3.70	1.10	80.1	22.8	6.73	2.34		
F-test	*		*	ns	ns	ns	ns	ns	ns	ns		
<u>Rate of N fertilizer</u>												
0 kg ha ⁻¹	6.16 b		12.5 c	3.19	3.77	1.12	87.1 a	24.0 a	6.46 b	2.27		
80 kg ha ⁻¹	6.71 a		13.8 b	3.11	3.66	1.11	80.5 ab	22.6 b	7.06 a	2.44		
160 kg ha ⁻¹	6.90 a		14.4 a	3.18	3.70	1.13	78.5 b	22.7 b	7.24 a	2.36		
F-test	***		***	ns	ns	ns	*	*	**	ns		
<u>Variety</u>												
Suwan 1	6.02 b		13.8 b	3.33 a	4.00 a	1.10 b	87.0 ab	24.7 a	6.64 b	2.66 a		
La Posta Sequia	6.62 b		13.7 b	3.03 b	3.63 b	1.10 b	74.6 c	21.8 b	6.66 b	2.38 ab		
KTX2602	6.16 b		15.0 a	3.28 a	3.57 b	1.18 a	88.0 a	23.1 ab	8.05 a	2.37 b		
DK888	7.56 a		11.9 c	3.02 b	3.63 b	1.09 b	78.5 bc	22.9 b	6.34 b	2.01 c		
F-test	***		***	***	***	**	***	***	***	***		

*, **, *** significant at P=0.05, 0.01, and 0.001, respectively. ns not significant.

[†] The effects of some two-way interactions were significant (see Tables 4 to 8); the effects of the remaining two-way interactions and all three-way interactions were not significant.

[‡] Means not followed by the same letter within a column are significantly different.

Table A.5: Main effects¹ of variety, water regime, and rate of N application on grain yield and concentrations of grain N and minerals in 1997.

	Grain yield		g kg ⁻¹							µg kg ⁻¹			
	Mg ha ⁻¹		N	P	K	Mg	Ca	Zn	Mn	Cu			
Grand mean	5.70		14.0	3.32	4.00	1.19	92.1	25.0	6.27	2.94			
<u>Water regime</u>													
Drought-stressed	5.02 b [‡]		13.9	3.29	4.00	1.18	95.8	24.5	6.24	2.97			
Well-watered	6.37 a		14.1	3.35	3.99	1.20	88.5	25.5	6.31	2.91			
F-test	**		ns	ns	ns	ns	ns	ns	ns	ns			
<u>Rate of N fertilizer</u>													
0 kg ha ⁻¹	4.46 b		12.6 c	3.32	4.03 a	1.17 b	98.6 a	26.4 a	6.02 b	2.97			
80 kg ha ⁻¹	6.14 a		14.2 b	3.29	3.94 a	1.19 ab	89.0 a	24.3 b	6.32 a	2.84			
160 kg ha ⁻¹	6.50 a		15.2 a	3.36	4.03 a	1.21 a	88.8 a	24.3 b	6.48 a	3.01			
F-test	***		***	ns	*	**	*	***	***	ns			
<u>Variety</u>													
Suwan 1	5.24 c		14.3 ab	3.37 b	4.13 a	1.15 b	91.0	26.5 a	6.10 c	3.32 a			
La Posta Sequia	5.66 b		14.0 b	3.18 c	3.99 b	1.17 b	88.9	23.4 c	6.37 b	2.74 b			
KTX2602	5.51 bc		14.7 a	3.58 a	3.98 b	1.30 a	95.4	26.3 ab	6.82 a	3.12 ab			
DK888	6.39 a		13.0 c	3.14 c	3.89 b	1.14 b	93.3	24.9 abc	5.81 d	2.58 b			
F-test	***		***	***	***	***	ns	***	***	**			

*, **, *** significant at P=0.05 and 0.01, respectively. ns not significant.

¹ The effects of some two-way interactions were significant (see Tables 4 to 8); the effects of the remaining two-way were not significant. The three-way interactions were not significant except for P.

[‡] Means not followed by the same letter within a column are significantly different.

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