CHAPTER 1

Literature Review

Effects of water stress on seed germination, seedling emergence and growth

Semi-arid areas are characterized by limited and erratic precipitation, frequently resulting in droughts at different periods during the growing season. Water stress is recognized as one of the most severe abiotic stresses influencing crop productivity in these areas (Blum, 1988). Most studies on drought tolerance have focused on the late vegetative and reproductive periods of growth, and the effects of drought during those periods on yield. However, since successful field establishment and vigorous stands contribute to higher yield, traits of drought tolerance should also include the ability of seeds to germinate and seedlings to develop under limited moisture availability (Baalbaki *et al*., 1999).

Soil water supply is an important environmental factor controlling germination and seedling emergence. Drought stress often limits germination and emergence in semi-arid regions either by delaying initiation of germination, by slowing the rate of germination or by decreasing final percentage germination (Hegarty, 1978; Kramer & Kozlowsky, 1979; Baalbaki *et al*., 1999). The reason for reduced germination under water stress conditions has been stated by Hadas (1976) to be the effect of low water potential on enzymatic activity, and not to limiting water uptake. Singh & Ambawatia (1988), on the other hand, indicated that low water uptake and restricted metabolic activities were causes for reduced germination under water stress. The research results of Gurmu & Naylor (1991) and Falleri (1994), however, attributed reduced germination to reduced water uptake. It is also evident from the results of Stout *et al*. (1980) that water uptake of two sorghum cultivars, germinated under a PEG 6000 induced stress, declined significantly from 0.40 and 0.35 g H_2O g^{-1} dry weight of seeds in water to 0.29-0.32 and 0.24 -0.30 g H_2O g^{-1} dry weight of seeds in stress levels ranging between –0.3 and –1.0 MPa. Decreased rate and percentage of

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germination due to drought stress have been reported for sorghum (Saint-Clair, 1976; Stout *et al*., 1980; Smith *et al*., 1989; Gurmu & Naylor, 1991), wheat (Lafond & Baker, 1986; Baalbaki *et al*., 1999), triticale (Gawronska & Grzelak, 1993), sunflower (Somers *et al*., 1983), mung bean (Fyfield & Gregory, 1989), pea (Singh *et al*., 1990), rice (Takaki, 1990) and tree legumes (Grouzis & Danthu, 2001).

The percentage and rate of germination of crop seeds are of considerable agronomic importance. Early and rapid germination is particularly important in areas where seedlings have a short time to develop (Fady, 1992). In this regard, the results of many studies indicate that the adverse effect of drought stress is more marked on the rate of germination than on germination percentage. For instance, Lafond & Baker (1986), Baalbaki *et al.* (1999) and Smith *et al.* (1989) reported reduced germination rate in wheat, sorghum and pearl millet as drought stress increased. Falleri (1994), in his evaluation of the germination performance of six provenances of *Pinus pinaster* Ait. under five water stress treatments (0, -0.2, -0.4, -0.6, and –0.8 MPa), also noticed more adverse effects of water stress on germination rate than on germination percentage. Stout *et al.* (1980), on the other hand, reported a delay in initiation of germination in sorghum cultivars under water stress. Gurmu & Naylor (1991) and Falleri (1994) have also reported that lower water potential reduced the seed water uptake leading to slower radicle and coleoptile emergence and extension. Similarly, reduction in the imbibition rate of pea seeds with increasing levels of PEG induced water stress where imbibition rate was reduced from nearly 80% in a no stress condition to nearly 25% at a water stress level of –0.5 MPa was reported by Singh *et al.* (1990).

According to Collis-George & Williams (1968), as cited by Fyfield & Gregory (1989), measurement of radicle lengths during germination experiments can be regarded as a growth parameter for the developing seedlings, in contrast to germination itself, which simply registers the arrival at a certain stage of development. In this regard, Fyfield & Gregory (1989) reported a slowdown in the rates of radicle elongation in mung bean as water potential decreased from 0 to –2.2 MPa. Similarly, Gurmu & Naylor (1991), in their study to compare the germination and early seedling growth of two contrasting sorghum cultivars under four water stress treatments (0, -0.45, -0.73, and –1.15 MPa), found decreased radicle elongation in both cultivars as water potential become lower. The results of Singh *et al.* (1990) also demonstrated that radicle length in peas declined from 5.3 cm in the control to 2.1 cm at –0.5 MPa. De Villalobos & Pelaez (2001) reported reduced radicle growth of Prosopis from 21 mm under no stress condition to 5 mm under water stress (-1.0 MPa). According to Hsiao (1973) reduction in the extent of radicle elongation under water stress can be attributed to a reduction in cell expansion. Several other researchers have also assessed the effect of water stress at germination on the plumule growth of several crop plants. In this respect Gawronska & Grzelak (1993) reported reduction in plumule length in triticale. They reported reductions of 25, 43, 62, and 73% in the length of seedlings (radicle plus plumule) as seeds were germinated at water potentials of –0.2, -0.4, -0.6, and –0.8 MPa, respectively. Singh *et al.* (1990) also noted significant reductions in the plumule length of peas with increasing levels of water stress in which the plumule length after seven days of growth declined from 7.5 cm in the control to 7.22, 6.78, 5.81, 5.01, and 4.67 cm at stress levels of -0.1, -0.2, -0.3, -0.4, and –0.5 MPa, respectively.

Several studies have illustrated the existence of inherent variation in germination and seedling emergence under water stress in many crop species. Mali *et al.* (1979) reported substantial differences between varieties in water uptake from soil by the time of germination, and also differences within varieties in the rate of and amount of uptake, according to the water potential of the soil. They drew attention to the possible agronomic value of genotypes which may take up sufficient water for germination when soil water availability is low. Cultivar differences in sorghum, with respect to the ability of seeds to germinate under water stress, have been previously described. Stout *et al.* (1980) demonstrated that cultivar NK300 had a faster rate and higher percentage germination than the cultivar M35. Gurmu & Naylor (1991) also found cultivar variability in sorghum, where cultivar Korokolo had higher percentages of radicle and coleoptile emergence than cultivar Ariana. Saint-Clair (1976) also demonstrated cultivar differences in sorghum in which five sorghum cultivars (CE-90, 69-4, RS626, NK300 and C-42Y) had better germination performance at the highest stress level out of 11 cultivars evaluated. Baalbaki *et al.* (1999) evaluated five wheat cultivars under five water stress treatments and found two cultivars (Salamouni and Cham-6) with higher percentage germination and two cultivars (Mexipak and Memof-2) with lower germination percentages.

Water deficit stress effects and variability of tolerance in sorghum cultivars

In areas of the semi-arid tropics where sorghum is widely grown, drought is often the main factor causing low yields (Matthews *et al.*, 1990). Most often water deficit affects plant water status, reducing the water potential and thus impairing many functions (Reddy & Reddi, 1992). Reduced plant water potential in turn results in reduced photosynthesis, increased stomatal diffusive resistance and consequently lower plant growth rate. Water stress can have major effects on the growth, development and yield of crop plants by affecting various physiological and morphological processes such as leaf area development, photosynthetic activity, transpiration, translocation of assimilates, leaf senescence, and stomatal conductance (Simpson, 1981). The adverse effects of water stress on one or more of these processes, on a tissue or whole plant level, reduces growth rate, carbohydrate partitioning and grain yield.

Plant growth rate under water deficit is affected in at least two ways: the rate of increase of leaf area is depressed by loss of turgor, and the rate of photosynthesis is decreased by the closing of the stomates (McCree, 1974). Lu & Neumann (1998) attributed growth inhibition, due to water deficit, to inhibition of cell expansion and new cell production. Similarly, Lorens *et al.* (1987) noted that water stress during vegetative development reduces expansion of leaves, stems, and roots and ultimately affects the development of reproductive organs and potential grain yield. The effect of water stress on the growth, development, and dry matter partitioning has been extensively studied. Bajj *et al.* (2000) reported reduced shoot and root fresh weights under PEG-induced water stress. Schulze (1986) also indicated changes in carbohydrate partitioning in crop plants due to water stress. Inuyama *et al.* (1976) noted reductions in sorghum plant height, stem length, head length and exertion length due to water deficit treatments. Blum *et al.* (1989) reported a 70% reduction in sorghum plant height as a result of water stress.

The effect of water deficit stress on leaf expansion and leaf area development, in several crop species is well documented (McCree & Davis, 1974; Turner & Begg, 1981; Parameswara & Krishnasastry, 1982; Garrity *et al.*, 1984; Rosenthal *et al.*, 1987). The production of dry matter by a crop depends on the solar energy that it captures and utilizes to convert carbon dioxide and water into dry matter. The capture of solar energy in turn depends on the interception of that energy by organs capable of photosynthesis. Thus, crop productivity depends on the development of leaf area to intercept radiant energy, and the rate of net photosynthesis to convert it into dry matter. Due to the fact that leaf area is the main site of assimilate production, the reduction in leaf area, due to water stress, strongly affects dry matter production (McCree & Davis, 1974; Garrity *et al.*, 1984).

The work of McCree & Davis (1974), Parameswara & Krishnasastry (1982) and Rosenthal *et al.* (1987) illustrated the adverse effects of water deficit stress on leaf area development. McCree & Davis (1974) reported a 40% reduction in sorghum leaf area as the atmospheric conditions changed from warm and humid to hot and dry conditions. According to Parameswara & Krishnasastry (1982) inhibition of leaf growth is often a primary whole plant response to moderate water deficit stress which indicates that leaf elongation is more sensitive to water deficit stress than most plant processes and can be severely inhibited at relatively low leaf water potentials. Similarly, Turner & Begg (1981) in their review indicated that water deficit stress at the vegetative stage results in smaller leaves. Water deficit also affects the total leaf number and rates of individual leaf emergence (Arkin *et al.*, 1983 cited by Rosenthal *et al.*, 1987), which determine the surface area available for transpiration and assimilate production (Myers *et al.*, 1984).

In comparing drought resistant (Gadambalia) and drought susceptible (Tabat) sorghum cultivars, Salih *et al.* (1999) reported a 13% reduction in leaf area in the susceptible line. Sivakumar *et al.* (1979) in comparing sorghum growth under irrigation and residual moisture, recorded reduced leaf area development in water stressed plants. Similarly, Rosenthal *et al.* (1987) reported reduced leaf area development and lower biomass yield, when plants were grown in soil where the plant available water was below 50%. Furthermore, Wright *et al.*, (1983) in their study on the response of two sorghum genotypes to five levels of water stress, produced evidence on a reduced rate of leaf area development due to water stress. Parameswara & Krishnasastry (1982) also observed a reduced leaf expansion rate in sorghum, which ultimately reduced leaf area and total biomass. The inhibition of cell division and cell enlargement are supposed reasons for reduced leaf area development of plants under water stress (McCree & Davis, 1974). Many researchers (McCree & Davis, 1974; Wright *et al.*, 1983; Rosenthal *et al.*, 1987; Santamaria *et* *al.*, 1990; Munamava & Riddoch, 2001) have demonstrated a reduction of leaf area in sorghum grown under water stress. Garrity *et al.* (1984) also measured a leaf area index as low as 1.28 in stressed sorghum as compared to 1.92 in unstressed plants.

Many research results have revealed that in addition to its effect on leaf area development and senescence, water stress also adversely affects the rate of net photosynthesis per unit area (Turner & Begg, 1981; Parameswara & Krishnasastry, 1982). The photosynthetic capacity of plants is determined primarily by the total leaf area and the activity of each leaf unit (Boyer & McPherson, 1975). Reduced leaf area development and decreased stomatal conductance are said to be the main causes of reduced net photosynthesis under water stress (Parameswara & Krishnasastry, 1982; Ludlow & Muchow, 1990; Jones, 1998). According to Turner & Begg (1981) the immediate response of net photosynthesis rate to water stress appears to be due to stomatal closure in most species. Boyer & McPherson (1975), in their review, indicated that the rate of photosynthesis in water stressed maize was only 15% of that in the well-watered control.

Soil water deficit has been also identified as a limiting factor affecting sorghum root development and distribution in the soil profile (Blum & Arkin, 1984). Many studies have illustrated this, with an increase in the root:shoot ratio of many crops with increasing water stress (Turner & Begg, 1981; Bajj *et al.*, 2000; Matsui & Singh, 2003). This could arise simply from a relatively greater decrease in shoot dry weight and greater allocation of the limited carbon available to roots (Hsiao & Acevedo, 1974; Bajj *et al.*, 2000).

The existing evidence indicates that a deficiency of water during any growth stage of sorghum often results in a loss of grain yield. The magnitude of the yield reduction, however, depends on the growth stage of the crop at the time of stress, the severity and duration of the stress, and the susceptibility of the genotype to stress (Lorens *et al.*, 1987). Several research results (Inuyama *et al.*, 1976; Garrity *et al.*, 1984; Rice & Eastin, 1986; Craufurd & Peacock, 1993; Craufurd *et al.*, 1993) have revealed that sorghum is particularly sensitive, in terms of seed number and yield losses, to stress during the boot stage, which is a period of rapid plant growth and panicle development. Besides, Mastrolilli *et al.*, (1995) indicated that water stress at the vegetative phase also influenced later development of the panicle and final yield.

In attempting to improve crop productivity in water-limited environments, a better understanding of plant responses and alternative tactics for coping with water stress provides a foundation for more efficient water management and exploiting genetic variability. The results of early research on the effects of water stress on plants have highlighted the various alterations in developmental, morphological and physiological mechanisms of crops to adapt to water deficits (Saneoka & Ogata, 1987). Thus, exploring the mechanisms enabling plants to adapt to water deficits has been a major goal of plant physiologists and breeders. Such efforts have resulted in identifying several mechanisms that enable sorghum to achieve economic yields under water-limited environments. Plant morphological and physiological traits that enable sorghum to adapt to drought stress and give higher yields include leaf rolling (Matthews *et al.*, 1990a), increased leaf reflectance (Ludlow & Muchow, 1990), epicuticular wax deposition (Jordan *et al.*, 1983; Cameron *et al.*, 2002; Kunst & Samuels, 2003), ability to maintain stomatal opening at low water potential (Turner, 1974; Stout & Simpson, 1978; Blum *et al.*, 1989; Ashraf & Ahmad, 1998), reduced stomatal number (Arnon, 1992), development of a large, vigorous root system (Nour & Weibel, 1978; Blum & Arkin, 1984; Bawazir & Idle, 1989; Soman & Seetharama, 1992; Salih *et al.*, 1999), maintenance of green leaf area (Duncan *et al.*, 1981; Xu *et al.*, 2000) and high osmotic adjustment or turgor maintenance (Ludlow *et al.*, 1990; Santamaria *et al.*, 1990; Al-Hamdani *et al.*, 1991; Tangpremsri *et al.*, 1991).

Various morphological characteristics of leaves help to reduce the transpiration rate and may affect plant performance and even survival under drought conditions. Leaves with thick cuticles, waxy surfaces, sunken stomata, and hairiness are common and effective (Arnon, 1992; Reddy & Reddi, 1992). Epicuticular wax deposition increases in drought stressed plants and has been identified as a selection criterion for drought tolerance. In sorghum it was found that increases in wax load were inversely correlated with rates of cuticular transpiration (Jordan *et al.*, 1984). Increased wax concentration also makes plants more tolerant of high temperature stress or of a combination of moisture and heat stress (McWhorter, 1993; Cameron *et al.*, 2002; Kunst & Samuels, 2003). Several lines of evidence suggest an association between drought resistance and epicuticular wax deposition for sorghum. Jordan *et al.* (1983) reported significant variability in average epicuticular wax loads among genotypes. Saneoka & Ogata (1987) also reported an increase in cuticular resistance of bloom lines of sorghum by 90% as compared with 15% in bloomless lines under water stress.

Development of extensive root systems is another mechanism of water stress avoidance in sorghum (Salih *et al*., 1999). A large and vigorous root system, through avoidance of plant water deficits, contributes to higher yields in water-limited environments (Ludlow & Muchow, 1990). Roots are usually the sites of the highest resistance in the pathway for liquid phase movement of water through the soil-plant-atmosphere continuum (Kramer & Boyer, 1995). The efficiency of soil water uptake by the root system is, therefore, a key factor in determining the rate of transpiration and tolerance to drought (Salih *et al*., 1999). Existing evidence (Nour & Weibel, 1978; Turner & Begg, 1981; Wright & Smith, 1983; Bajj *et al*., 2000) indicates that greater partitioning of dry matter to the root system would enable better exploration of soil water reserves and may, therefore, confer increased drought resistance. The development of vigorous root systems by drought resistant crop strains was illustrated by the work of Bhan *et al*. (1973) and Bajj *et al*. (2000) who found greater root weights and higher root:shoot ratios in drought resistant strains of sorghum and wheat than in drought susceptible lines.

Several strategies have been devised to mitigate the impact of drought stress on crop production systems in semi-arid areas. Selection of plant species with drought resistance attributes has been considered an economic and efficient means of achieving these objectives (Ashraf *et al*., 1992). The available evidence indicates that there is considerable genetic variation in sorghum when it comes to those aspects of the plant that confer adaptation to drought stress (Blum *et al*., 1989; Donatelli *et al*., 1992; Blum, 1993). According to Blum *et al*. (1989) and Blum (1993), sorghum genotypes were found to differ in terms of nearly all the recognized drought resistance mechanisms. Matthews *et al*. (1990b) reported a higher leaf water potential in drought resistant sorghum lines and a lower leaf conductance in the susceptible lines. Wright *et al*. (1983), Kidambi *et al*. (1990), Santamaria *et al*. (1990) and Donatelli *et al*. (1992) have all reported genotypic variability in tolerance to drought stress after comparing a wide range of sorghum genotypes. Stout & Simpson (1978) also noted distinct cultivar responses in leaf growth in response to drought stress. In one of their varieties, M-35, water stress extended the period of leaf and stem growth, and delayed inflorescence development, but in another variety, NK 300, the leaf and stem growth period was shortened and inflorescence development advanced. Salih *et al.* (1999) comparing drought susceptible and resistant sorghum cultivars, obtained a 30% reduction in root density and a 31% reduction in nodal roots in the susceptible cultivar, while it was not affected in the resistant one. Soman & Seetharama (1992) also reported genotypic variation in the rate of nodal root elongation. Henzell *et al.* (1976) studied stomatal sensitivity to leaf water deficit in nine genotypes and found significant differences between genotypes for stomatal diffusive conductance. Where stomatal conductance in the sensitive genotypes (Alpha and Shallu) decreased rapidly as leaf water potential declined due to water stress, it declined more slowly in the tolerant genotypes (I.S.1598C and M35-1).

The importance of relative water content of leaf material as a selection criterion is widely recognized. Work done by Clarke & McCaig (1982) and Schonfeld *et al.* (1988) indicated that cultivars that maintain high leaf RWC during drought stress are more drought tolerant. Changes in the RWC of leaves are considered a sensitive indicator of drought stress (Strauss & Agenbag, 2000). Strauss & Agenbag (2000), in comparing different wheat cultivars, observed decreased RWC in stressed treatments compared to the control. It can be concluded that by measuring different physiological and morphological responses under different water stress conditions, it would be possible to evaluate essential traits and select drought tolerant cultivars.

Impact of the interactive effects of moisture conservation, nitrogen fertilization and cultivars on the growth, development and nutrient use efficiency of sorghum

In semi-arid areas water is often a limiting factor for crop production. If it were possible to retain and utilize all the rainfall received, crop losses due to water stress would be reduced. Tied-ridging (ridge and furrow system) is a technique developed for *in-situ* rainwater harvesting in semi-arid areas. It is widely used in the semi-arid areas of many African countries (Jones & Clark, 1987). Tied-ridging is a technique of forming micro basins for impounding runoff, thereby increasing the opportunity time for water to infiltrate (Hulugalle, 1987; Wiyo & Feyen, 1999). Available research evidence in Botswana (Carter & Miller, 1991), Zimbabwe (Piha, 1993; Vogel, 1993), Burkina Faso (Hulugalle *et al.*, 1990), Malawi (Wiyo & Feyen, 1999; Wiyo *et al.*, 2000) and USA (Krishna, 1989) have documented the effectiveness of tied-ridges in reducing surface runoff and increasing soil water storage. For instance, Njihia (1979) reported a reduction of runoff from 38-43%, with flat planting, to 1.2 – 4.7% with tied-ridges. Jones & Clark (1987), in the USA, observed retention of 25 to 30 mm of runoff per annum with tied-ridges. Hulugalle (1987) also observed increased profile water content, by an average of 24.6 and 30.5 mm per week, by using tied-ridges. Selvaraju *et al.* (1999) reported a 14% increase in soil water content with tied-ridges compared to flat beds. In semi-arid areas of NE Ethiopia, tied-ridging has a large potential to mitigate the devastating effect of drought stress through reduced runoff and improved retention of rainwater.

Through reducing runoff and increasing moisture availability, tied-ridges can substantially improve the growth and development and grain yield of several crops (Reddy & Kidane, 1993; Wiggins, 1995). For instance, Wiggins (1995) observed significantly greater root length, plant height, leaf and tiller number and fresh and dry weight of sorghum in ridge plantings compared with flatbed planting. Hulugalle (1987) also reported increased root growth in cowpeas planted in tied-ridges. Kanton *et al.* (2000) obtained superior grain yields from tied-ridge planting (54 – 175%) compared to sowing on the flat. Jones & Clark (1987) realized a sorghum yield increase of 2460 kg ha^{-1} from tied-ridging. The work of many other researchers (Gerard *et al.*, 1984; Saleem *et al.*, 1987; Belay *et al.*, 1998; Kanton *et al.*, 2000; Jensen *et al.*, 2003) have also illustrated many-fold grain yield increases in several crops.

It has been indicated that the vigorous root system development under ridges can enable plants to explore larger volumes of soil which in turn can lead to improved uptake of water and nutrients (Selvaraju *et al.*, 1999). In this regard, Gordon *et al.* (1993) found higher total N uptake in the ridge system (126 kg ha^{-1}) compared with chisel (102 kg ha^{-1}) and moldboard (106 kg ha^{-1}) tillage systems. They also observed a higher apparent N recovery in the ridge system than in the other two tillage systems. The higher N uptake and recovery in the ridge system was attributed to the greater amount of soil water availability.

Apart from the effects of drought stress, the growth, development and yield of sorghum are also strongly affected by poor soil fertility. The problem of nitrogen deficiency is often acute in semi-arid areas where soils typically have low organic matter contents (Broadbent, 1981). Nitrogen deficit is the most severe and widespread nutrient constraint limiting sorghum productivity in NE Ethiopia (Bayu *et al*., 2002). Mamo *et al*. (1988) reported that due to a long cropping history and low manure and fertilizer inputs, the nutrient status of Ethiopian soils is generally low and nitrogen is the most limiting nutrient for crop production. It is well known that many physiological processes associated with crop growth are enhanced by N supply (Eck, 1984; Muchow, 1998). Nitrogen plays a central role in plant biochemistry as an essential constituent of cytoplasmic proteins, nucleic acids, chlorophyll, cell walls and a vast array of other cell components. Consequently, a deficiency in the supply of nitrogen has a profound influence upon crop growth and can lead to a total loss of grain yield in extreme cases (Hay &Walker, 1989). Numerous studies have shown the limiting effects of N deficiency on the growth and development of crop plants (Muchow, 1988; Muchow & Davis, 1988; Muchow, 1990; McCullough *et al*., 1994; Muchow, 1994). Delayed phenological development in response to N deficiencies has also been illustrated by many research results. Muchow (1990 & 1994) and Kamoshita *et al*. (1998) observed delayed anthesis and maturity in sorghum and maize. Muchow (1988, 1989) and McCullough *et al*. (1994) observed reduced plant growth and development arising from reduced leaf emergence rate and leaf area development. The adverse effects of N deficiency on plant height, shoot weight, plant N uptake, leaf area index, leaf area duration, crop photosynthetic rate, radiation interception (PRI) and radiation use efficiency (RUE) are well documented in the review of Novoa & Loomis (1981) and the work of many others (Muchow, 1988; Muchow & Davis, 1988; Youngquist & Maranville, 1992; Pandey *et al*., 2000; Van Oosterom *et al*., 2001). Biomass production, which is largely dependent on leaf area index, is also strongly dependent on leaf N (Muchow & Davis, 1988; Muchow & Sinclair, 1994).

Thus, improving crop production and productivity in these areas requires the use of nitrogen fertilizer, with great emphasis on the efficiency of N utilization. Considering the high cost and the detrimental effects of nitrogen deficiencies on crop production, the efficient use of nitrogen in crop production has become a desirable agronomic, economic, and environmental goal (Le Gouis *et al*., 2000). Nitrogen use efficiency could be improved through improved agronomic practices and through growing cultivars efficient in nutrient use. Many soil, plant and other environmental factors affect nitrogen use efficiency (NUE). Environmental factors such as rainfall also affects nutrient use efficiency. Water limitations affect N-related traits such as N content, N utilization, and N harvest index in crop plants (Zweifel *et al*., 1987; Bennett *et al*., 1989). The availability, movement and uptake of nutrients are affected by moisture availability. For instance, Pandey *et al*. (2000) observed decreased N uptake in maize under deficit irrigation. Nonetheless, various plant characteristics have been suggested to be important in the acquisition and utilization of nitrogen (Stewart, 1991). For instance, Mengal (1983) indicated that NUE is related to crop morphological and physiological traits. Similarly, Lafever (1981) and Jackson *et al*. (1986) as cited by Akintoye *et al*. (1999) indicated that the differences in genotypic responses to nutrient stresses are affected by several crop traits including root morphology and extension, and biochemical and physiological mechanisms involved in nitrate assimilation and use. This indicates that selecting cultivars with vigorous root growth can lead to more efficient recovery of applied fertilizers.

The existence of genotypic differences in terms of N uptake, partitioning and NUE have been reported for several crops including sorghum (Maranville *et al*., 1980; Pal *et al*., 1983; Youngquist & Maranville, 1992; Gardner *et al*., 1994; Buah *et al*., 1998; Traore & Maranville, 1999), maize (Ma & Dwyer, 1998; Akintoye *et al*., 1999; Ma *et al*., 1999) and wheat (Cox *et al*., 1985; Van Sanford & MacKown, 1987; Dhugga & Waines, 1989). For instance, Buah *et al*. (1998) evaluated the agronomic responsiveness of 13 sorghum genotypes, differing in NUE, to three N rates (0, 50 & 100 kg N ha^{-1}) and observed greater yields in the high NUE sorghum types than in the low NUE types. This was attributed to differences in the efficiency of recovery of applied N fertilizer. Muchow (1998) cited the work of Kamoshita *et al*. (1996) where they examined the extent of genotypic variation in grain sorghum under variable water and N supply, and found significant variation among 14 hybrids in grain yield, NUE and grain N concentration. Ma *et al*. (1999) also observed variation in N uptake in two maize hybrids where Pioneer 3902 accumulated 60 to 160 kg N ha^{-1} in the grain as compared to 40 to 110 kg N ha^{-1} for Pride 5. McCullough *et al*. (1994) also evaluated the same hybrids for their N uptake, partitioning and NUE and observed higher NUE for Pioneer 3902 than Pride 5 under the lowest N supply. Traore & Maranville (1999), comparing the nitrate *reductase* activity in seven sorghum genotypes, found greater pre-anthesis nitrogen uptake, accumulation and NUE in tropical lines than in hybrids and U.S. adapted lines. Akintoye *et al*. (1999) found variability among 10 maize lines in N uptake, utilization, NUE and N harvest index. Hibberd & Hall (1990) compared the NUE of two sorghum hybrids under irrigation and rainfed conditions and observed varietal differences with regard to N use, where variety Goldfinger was superior to variety E-57. Prolonged maintenance of green leaf area for photosynthate production during grain filling and the ability to take up available soil N during grain filling, are traits that can facilitate greater NUE. In this regard, Ma & Dwyer (1998) assessed N uptake and utilization in two maize hybrids and noted greater NUE and uptake in the "stay-green" hybrid (Pioneer 3902). However, selection of genotypes with efficient N use could be complicated by their interaction with management practices (Zweifel *et al*., 1987). Uptake and utilization of N is dependent upon genotype, plant age, available N in the soil, and other environmental parameters that influence plant growth (Youngquist & Maranville, 1992). For instance, Hirel *et al*. (2001) indicated that expression of genetic variability for the components of NUE is largely dependent on the level of nitrogen fertilizers supplied to the crop. Thus, the development of cultivars with predictable N use efficiency requires an understanding of how various production environments affect genotypic N utilization.

Many studies have also reported genotypic differences in dry matter production and partitioning in response to nitrogen fertilizer. Utzurrum *et al*. (1998) found differences in dry matter accumulation between two sorghum hybrids in response to N application, where Y3 produced significantly more total dry matter than X3. Maman *et al*., (1999) also observed differences in dry matter accumulation between pearl millet genotypes in response to N fertilization. Similarly, Greef *et al*. (1999) compared eight forage maize cultivars and observed variability among the cultivars for dry matter production in response to N fertilization. Hons *et al*. (1986) observed variations among sorghum hybrids in height, leaf number and leaf area index (LAI) in response to fertilization. Pal *et al*. (1983) obtained 20% more dry matter per plant in sorghum supplied with 129 kg N ha^{-1} than the ones supplied with 80 kg N ha^{-1}. The physiological processes of carbohydrate partitioning and N metabolism are associated. Thus, genotypes with differences in grain yield potential may differ in N accumulation and NUE (Buah *et al*., 1998). This review suggests that by adopting moisture conservation practices, applying nitrogen fertilizer and selecting nitrogen efficient cultivars the productivity of crops could be enhanced in drought stressed semi-arid areas.

Integrated use of farmyard manure and inorganic fertilizers in the improvement of soil fertility and crop yield

The farming systems in NE Ethiopia generally do not include crop rotation and fallowing due to rapid population growth. Continuous and intensive cropping, without the restoration of the soil fertility, is the dominant feature of the farming systems. Consequently, the inherent fertility status of the soils in these areas has been dangerously depleted (Georgis & Alemu, 1994). Increasing crop production on such degraded soils, therefore, becomes an enormous challenge. Soil fertility depletion in smallholder farms of Africa, including Ethiopia, is recognized as the fundamental biophysical limiting factor responsible for the declining per-capita food production of the continent (Alexandratos, 1995; Smaling & Braun, 1996; Sanchez & Leakey, 1997). Studies in other parts of the continent have revealed that the magnitude of soil nutrient mining is huge on small-scale farms (Stoorvogel *et al*., 1993; Bationo *et al*., 1998; De Jager *et al*., 1998; Nandwa & Bekunda, 1998; Van den Bosch *et al*., 1998). It could be even worse in the densely populated countries like Ethiopia, Kenya, Malawi and Rwanda (Stoorvogel *et al*., 1993; Smaling *et al*., 1997).

A basic challenge to agricultural research and development is to better understand and arrest this trend. To increase food production in Africa, a sustainable soil fertility replenishment strategy must be implemented that has the potential to supply nutrients and to arrest the mining of soil fertility taking place (Stangel *et al*., 1994). The soils of NE Ethiopia can no longer be productive with the existing fertility status. Thus, to increase food production on the existing degraded soils, inexpensive soil fertility replenishment technologies need to be available to the resource poor small-scale farmers. A key resource that could be useful in achieving a sustainable soil fertility management system is animal manure, which is important in maintaining soil quality through replenishing the organic matter content of the soil (Murwira *et al*., 1995). According to Carter *et al*. (1992), the use of animal manure to improve soil fertility and crop yield assumes particular importance where financial or logistic constraints on the availability of inorganic fertilizers exist, and where inherently infertile soils are used for the continuous production of grain crops.

The use of animal manure for the improvement of soil condition and crop yields is an ancient practice and is an integral part of many low-input farming systems (Francis *et al.*, 1990). The application of animal manure generally aims at two major goals: (i) increased supply of nutrients to the crop and (ii) increasing organic matter content in the soil, resulting in more favourable soil physical and chemical properties (De Ridder & Van Keulen, 1990). Animal manures provide N, P, K and other mineral nutrients (Lupwayi *et al.*, 2000; Hoffmann *et al.*, 2001). According to De Ridder and Van Keulen (1990) and Eck & Stewart (1995), manure can contain, on average 2.0, 0.5 and 1.5% (on dry weight basis) of N, P and K respectively, as well as significant amounts of Ca, Mg, Na and many of the trace elements.

Significant increases in total and NH_4^+- and NO_3^--N contents of the soil with addition of animal manure have been reported by several researchers in Africa (Powell, 1986; Kaihura *et al.*, 1999; Warman & Cooper, 2000; Hoffmann *et al.*, 2001). The addition of animal manure also increases the availability and mobility of P (Meek *et al.*, 1982; Powell, 1986). Organic anions formed during the decomposition of animal manure can compete with P for the same sorption sites and thereby increases P availability in the soil (Reddy *et al.*, 1999). Animal manure applications also result in a build up of exchangeable K and Mg (Meek *et al.*, 1982; Lupwayi & Haque, 1999). In Nigeria, Powell (1986) analyzed N and P balances after maize crops in an animal manuring study and found a three-fold increase in N in manured plots (128 kg ha^{-1}) as compared to the non-manured plots (42 kg ha^{-1}). Similarly, in Ethiopia the application of cattle manure to maize in a hedgerow intercropping system reversed nutrient balances from net negative balances of –7 to –19 kg N ha^{-1}, – 4 to –12 kg P ha^{-1} and –10 to –26 kg K ha^{-1}, where no nutrients were applied, to net positive balances of 59 to 62 kg N ha^{-1}, 9 to 35 kg P ha^{-1} and 74 to 80 kg K ha^{-1}, where 3 t ha^{-1} dry cattle manure was applied (Lupwayi & Haque, 1999). Significant increases in soil total N and available P and K from farmyard manure applications were also reported in Ghana (Kwakye, 1988) and Nigeria (Agbenin & Goladi, 1997). The restoration of soil nutrients and other soil fertility parameters by animal manure additions was also illustrated by data from Niger (Bationo & Mokwunye, 1991) in which the N and P content of the soil was significantly elevated when the soil was analyzed after two years of manure applications. In Tanzania, in a study conducted at eight locations, Kaihura *et al.* (1999) reported an increase in soil N level by 0.03%, P by six-fold and K by two-fold as a result of animal manure applications. Improvements in the soil chemical quality, with farmyard manure addition, can be explained by its potential to release CO_2, NH_4^+, NO_3^-, PO_4^- and undecomposed humic products to the soil through mineralization (Stevenson, 1994 as cited by Kaihura *et al*., 1999).

Unlike the commonly used commercial fertilizers, one of the benefits of fertilizing with animal manure is the provision of secondary nutrients. This was illustrated by the data of Warman & Cooper (2000) who found higher levels of B, Cu, Fe, Mn and Zn in manured than in unmanured soils after three years of fresh and composted manure applications at rates ranging from 5 to 10 t ha^{-1}. Similarly in a greenhouse study in Egypt, Abou-ElNaga *et al*. (1996) found increased availability of Mn and Zn with applications of farmyard manure at rates ranging from 0 to 238 m^3 ha^{-1}. In Tanzania, Kaihura *et al*. (1999) found a significantly increased level of Mg in manured plots (0.72-2.53 cmol kg^{-1}) as compared to farmers practice (0.38-2.04 cmol kg^{-1}) and inorganic fertilizer (N and P) application (0.48-2.13 cmol kg^{-1}).

The available evidence indicates that animal manure amendments can increase the pH of acid soils and decrease that of calcareous soils (Lungu *et al*., 1993; Wong *et al*., 1998; Hoffmann *et al*., 2001; Whalen *et al*., 2002). The reaction of acid soils, with applications of composts and animal manure, results in increased soil pH and decreased Al saturation (Hue, 1992). Animal manure applications supply important elements like K, Mg and Ca, which contribute to maintaining base saturation at higher levels (De Ridder & Van Keulen, 1990). The mechanism resulting in increased soil pH during organic manure additions is not fully understood but is thought to be due to specific adsorption of organic anions and the corresponding release of hydroxyl ions (Hue, 1992). Lungu *et al*. (1993) compared the effects of lime and farmyard manure application in correcting soil acidity and found a reduction in exchangeable Al of at least 50% above the values obtained with lime alone, and an increase of one unit in the pH of the topsoil with farmyard manure application. With 6 t lime ha^{-1} the reduction in exchangeable Al compared to the control was 36-52%, but the corresponding reduction with 30 t ha^{-1} farmyard manure application was 71-80%. In Nigeria, Powell (1986) reported an increase in soil pH on manured plots (pH 5.8) as compared to non-manured plots (pH 5.1). A similar effect has been reported in Ghana (Kwakye, 1988), Rwanda (Rutunga *et al*., 1998), Tanzania (Kaihura *et al*., 1999) and Canada (Whalen *et al*., 2002).

Other important soil chemical properties affected by animal manure applications include the cation exchange capacity (CEC), electrical conductivity and sodium adsorption ratio (Powell, 1986; De Ridder & Van Keulen, 1990; Hoffmann *et al*., 2001). In a long-term experiment established in 1960 in Burkina Faso the CEC of the soil increased with manure addition (especially at the higher rate) while in the fertilizer only plots the CEC remained unchanged. Similarly, in Nigeria in a savanna alfisol cultivated continuously for 45 years, Goladi & Agbenin (1997) reported an increase in CEC with farmyard manure application as compared to inorganic fertilizer.

Regular manure addition to arable soil either increases its organic matter content or reduces its rate of loss (Powell, 1986; De Ridder & Van Keulen, 1990; Schjonning *et al*., 1994; Eck & Stewart, 1995; Palm *et al*., 1997; Haynes & Naidu, 1998; Hoffmann *et al*., 2001). Mokwunye (1991) reported that application of manure in Nigeria once every three years at rates of 5 and 20 t ha^{-1}, resulted in a two-fold increase in soil organic matter levels in the first three years of the study, as compared to the non-fertilized plots. Soil organic matter level in the manured plots was also significantly superior to mineral fertilizer treated plots. Similar effects of farmyard manure on the level of soil organic matter in many African soils were reported by several researchers (Agbenin & Goladi, 1997; Goladi & Agbenin, 1997; Rutunga *et al*., 1998; Kaihura *et al*., 1999). Shirani *et al*. (2002) also reported a significant increase in soil organic matter content, ranging from 7.6 g kg^{-1} in the control to 24.5 and 38.4 g kg^{-1}, at 30 and 60 t manure ha^{-1}.

The maintenance of soil organic matter, by adding animal manure, has important benefits such as retention and storage of nutrients, increased buffering capacity in low activity clay soils, increased aggregate stability, improved soil macro-structure, improved infiltration, improved water holding capacity, erosion resistance and prevention of soil hardening (De Ridder & Van Keulen, 1990; Bationo & Mokwunye, 1991; Schjonning *et al*., 1994; Hoffmann *et al*., 2001). The application of animal manure has been found to increase the water holding capacity of soils (Girma & Endale, 1995). Powell (1986) also reported a 1% greater available water capacity and 2% greater water holding capacity in manured plots over non-manured plots, in Nigeria. A much more significant effect of manure addition on the water holding capacity of sandy soils was reported by Carter *et al*. (1992) in Botswana who reported 19 and 27% increases after four years of manure addition at the rate of 9 t ha^{-1}.

By improving the chemical and physical properties of the soil, application of animal manure often results in improved growth, development and yield of crops. Several studies have reported substantial yield increases from animal manure applications (Ikombo, 1984; Powell, 1986; De Ridder & Van Keulen, 1990; Lungu *et al*., 1993; Gibberd, 1995; Bekunda *et al*., 1997; Kaihura *et al*., 1999; Satyanarayana *et al*., 2002), although crop responses were found to be variable, and effects were highly site- and season-specific (Carter *et al*., 1992). In an experiment conducted in Niger, Bationo & Mokwunye (1991) reported a doubling of millet yield after one year of application at the rate of 5 t ha^{-1}. Similarly, Powell (1986) indicated that in Central Nigeria annual animal manure applications, at 3 t ha^{-1}, were found to be sufficient to maintain sorghum and millet yields at the same levels as those obtained after three years of fallow. In another study, in the semi-arid areas of West Africa, De Ridder & Van Keulen (1990) reported substantial increases in millet yield by applying animal manure. Similarly, in Nigeria Powell (1986) reported a 1 t ha^{-1} maize grain yield increase in manured plots over the non-manured plots. In eastern Kenya, Ikombo (1984) reported high and consistent maize yields with manure additions of 8 t ha^{-1}, which is close to that obtained by applying mineral fertilizer at the rates of 40 kg N ha^{-1} and 17 kg P ha^{-1}. In another study in Kenya, Gibberd (1995) reported a 58% yield increase in pure crops and a 75% yield increase in intercrops following animal manure application at the rates of 5 and 10 t ha^{-1}. In Tanzania, Kaihura *et al*. (1999) reported maize grain yield increases of 1732 kg ha^{-1} across eight locations with animal manure application. In India, Satyanarayana *et al*. (2002) reported a 25% increase in rice yields with the application of farmyard manure at the rate of 10 t ha^{-1}. Similarly, in Ghana significant sorghum and millet grain yield increases were reported with the application of manure at 10 t ha^{-1} (Kwakye, 1988). In Egypt, several researchers (El-Attar *et al*., 1982; Attia, 1999; Hegazi *et al*., 1999; Mohamed & ElAref, 1999) have also reported increased grain yields of various crops with the addition of varying rates of farmyard manure over the control and mineral fertilizer application. These results suggest that farmyard manures provide growth factors and microelements in addition to supplying the major nutrients (Badaruddin *et al*., 1999).

In the preceding sections the relevance of animal manure in restoring soil fertility has been clearly demonstrated, however, animal manure cannot meet crop nutrient demand over large areas because of the limited quantities available and the relatively low nutrient content of the material (Palm *et al*., 1997; Bationo *et al*., 1998; Brouwer & Powell, 1998). Larger amounts of animal manure than of mineral fertilizers are required, as their elemental concentrations are lower than that of mineral fertilizers (De Ridder & Van Keulen, 1990). Moreover, the rate of nutrient release from animal manure is slower, as the organic material must be decomposed to release the nutrient elements, which might lead to nutrient deficient periods (De Ridder & Van Keulen, 1990). On the other hand, although application of mineral fertilizers is an efficient means of increasing yields in arable farming systems, mineral fertilizers alone cannot sustain yields in the long run due to deterioration in soil organic matter content and soil acidification (Bationo *et al*., 1998).

Under smallholder conditions it is rarely possible either to purchase mineral fertilizer or generate animal manure to meet the rates reported in research studies (Bekunda *et al*., 1997). Thus, the combined use of animal manure and mineral fertilizers is often suggested as a promising alternative to smallholder farmers in Africa (Palm *et al*., 1997; Bationo *et al*., 1998). Since the rate of decomposition of manure, and the mineralization of nutrients contained in it, can be fairly slow, complementary use of inorganic fertilizers is essential to hasten the decomposition process. The beneficial effects of the combined use of organic and inorganic nutrients have been repeatedly shown in field trials (Palm *et al*., 1997). Available information indicates that high and sustainable crop yields can be obtained with judicious and balanced N, P, K fertilization, combined with organic material amendments. Effectiveness of mineral fertilizers is greatly enhanced when they are used in conjunction with organic amendments such as animal manure (Lal, 1993). It is commonly believed that combining organic with inorganic fertilizer will increase synchrony and reduce nutrient losses (Kramer *et al*., 2002). This is important not only in enhancing the efficiency of the fertilizers but also in reducing environmental problems that may arise from their use.

Effect of nitrogen fertilizer and planting density on the growth, development and yield of sorghum

Establishment of optimum plant population densities in different regions is essential to obtain maximum yields. Especially in crops grown on stored or conserved soil moisture under rainfed conditions, optimising the population density is critical as too high population densities can result in the depletion of most of the moisture before the crop matures, and too low population densities may leave moisture unutilised (Reddy & Reddi, 1992). The optimum plant population density for any crop varies considerably according to the environment under which it is grown. For instance, a dense plant stand is necessary in a fertile soil to fully utilize the available nutrients in the soil to realize potential yields. In contrast, higher plant populations under low fertility conditions can lead to development of nutrient deficiencies. Many workers have indicated that optimum planting densities for grain production are lower when water and nutrients are in short supply (Novoa & Loomis, 1981; Arnon, 1992). For instance, Hussein *et al*. (2000), studying plant density in maize under different amounts of seasonal rainfall, reported that during seasons of high rainfall (>600 mm in the growing season), each 10 000 increase in plants, up to 80 000 plants ha^{-1}, increased yield by 200 to 300 kg ha^{-1}. But during dry seasons, increasing plant population over 50 000 ha^{-1}decreased grain yields by 5 to 16%.

Plant density strongly affects leaf area, and therefore light interception and canopy photosynthesis (Gan *et al*., 2002). Investigations of the influence of population density upon crop dry matter yield have generally shown increases up to a plateau value at moderate densities and a significant reduction in production only at very high densities (Donald, 1963 as cited by Hay & Walker, 1989). The level of the plateau yield and the population density at which it is achieved depend on other factors, particularly the nitrogen supply (Hay & Walker, 1989). Dry matter production is directly related to the utilization of solar radiation, which is influenced by canopy development. Canopy light interception and photosynthesis are closely related to LAI up to a critical LAI, that which is required to intercept 95 % incident irradiance (Modarres *et al*., 1998).

The primary effect of increasing plant population density is to increase competition between adjacent plants. The resultant shading of plant tissues has a profound influence upon the balance of plant growth regulators, notably an increase in tissue levels of gibberellins, the overall effects of which are the promotion of leaf sheath and blade extension and the acceleration of all crop development processes. Thus, closer spacing of cereal plants is associated with larger and more rapidly growing leaf canopies, however, this effect is relatively short-lived because later leaves are smaller and the senescence of the leaf canopy is also faster (Hay & Walker, 1989).

The challenge to agronomists is to reconcile the requirements of optimising radiant energy interception and water use efficiency by manipulating inputs like plant population and nitrogen fertilizer. The total amount of biomass produced by a crop is determined by the crop growth rate and the duration of growth. Crop growth rate, in turn, is the product of net assimilation rate and LAI. In most crops, planting density is a major determinant of LAI (Van Averbeke & Marais, 1992). Novoa & Loomis (1981) have also indicated that leaf area is the main factor in biomass formation, and that it varies with plant population. Modarres *et al.* (1998) indicated that increasing the plant density is one management tool for increasing the capture of solar radiation within the canopy. Van Averbeke & Marais (1992) indicated that higher critical LAI values obtained by increasing planting density resulted in higher crop growth rates during grain filling, and consequently in higher grain yields. Tetio-Kagho & Gardner (1988) reported an increase in critical LAI from 2.6 to 4.0 by increasing planting density of maize from 35 000 to 63 000 plants ha^{-1}.

In maize, Tetio-Kagho & Gardner (1988) indicated that dry matter accumulation per unit area increased with increasing planting density and LAI until light is completely absorbed. In semi-arid conditions, the optimum LAI is determined by the amount of water available to the crop, and a LAI much lower than the critical LAI will be required. Grain yields have been found to increase with an increase in planting density up to an optimum density and to decline as planting density is increased above that optimum. Excessive population pressure has been shown to interfere with seed set producing lighter and fewer grains per head, which depresses total grain yield (Stewart & Lenga, 1982). On the other hand Berenguer & Faci (2001) indicated that at low planting densities yield could be compensated by an increase in the number of grains per panicle and high weight of grain. As plant density increases, changes may occur in the allocation of assimilates to different parts of the plant, as a result of which a greater proportion of the reproductive parts of an individual plant may become barren. For instance, Ogunlela & Okoh (1989) reported a significant increase in panicle weight, grain and straw yields in three sorghum varieties by increasing plant density from 33 300 to 50 000 plants ha^{-1}, but at 66,600 plants ha^{-1} these parameters declined significantly. Under very high population density levels, plants become barren. Van Averbeke & Marais (1994) reported a lower harvest index and an increase in barren plants in maize with increased population density above an optimum density under limited water supply, whereas, with a lower population density, competition is absent during the early stages of growth, as a result more flowers are initiated per plant. The load of inflorescence is more, which leads to competition among inflorescences of the plant. This loss of efficiency at the widest spacing is evident in fewer seeds per inflorescence and reduced seed size compared with more dense stands. In moderately dense stands, as a result of inter-plant competition at the time of flower initiation, the numbers of flowers produced are reduced and the plant is capable of filling all the seeds that set. The seeds per inflorescence and size of seeds per unit area are more in such conditions (Reddy & Reddi, 1992). Similarly, Berenguar & Faci (2001) found that at a low planting density yield could be compensated for by an increase in the number of grains per panicle, and increased size of the grain. Jones & Johnson (1991) have indicated that sorghum plants adjust yield components so that yields are maintained over a wide range of populations. Duncan (1984) reported that grain yield increased with an increase in planting density up to an optimum density and declined as planting density increased above the optimum. Decreases in the yield of individual plants at high population densities in crops like sorghum are due to the reduced size of panicles. Early maturing sorghum genotypes produce smaller and fewer functional leaves in which an increase in plant population should enable them to develop a large leaf area (Villar *et al*., 1989).

High plant population densities bring out certain modifications in the growth of plants. Plant height increases with increase in plant population due to competition for light. Sometimes it may happen that a moderate increase in plant population may not increase but decrease plant height, due to competition for water and nutrients but not for light (Reddy & Reddi, 1992). According to Reddy & Reddi (1992) increases in plant height due to higher population densities are advantageous for better light interception due to exposure of individual leaves over a wider vertical interval. Another adaptation of dense plant stands is the reduction in leaf thickness. Leaf orientation is also altered due to population pressure. The leaves tend to be more erect, narrower and arranged at longer vertical intervals under high plant densities (Reddy & Reddi, 1992). These are desirable architectural features to intercept more light.

Improvement in the productivity of dryland sorghum may be possible by manipulating agronomic practices like plant population. The productivity response and the compensation phenomena between the yield components of sorghum sown at different densities under variable nitrogen fertilizer supply are not well documented for the semi-arid areas of NE Ethiopia.

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