GENETIC AND PHYSIOLOGICAL STUDIES ON DROUGHT RESISTANCE TRAITS IN DRY BEAN (*Phaseolus vulgaris* L.) IN KENYA

BY

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DECLARATION

This thesis is my original work and has not been presented

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DEDICATION

To

My late grandparents

Mr.Kipsugut Arap Cheruiyot

and

Mrs.Tabaroon Cheruiyot

ABSTRACT

Field and trough studies were conducted to evaluate response of physiological and morphological traits of dry bean (*Phaseolus vulgaris* L.) genotypes to water stress over a period of two seasons. Thirty six bean genotypes were subjected to two watering levels (irrigated and not irrigated). Relative water content (RWC), leaf water potential (LWP), relative growth rate (RGR), days to 50% flower (DTF), taproot length (TRL) and root dry weight (RDW) were measured. High and low scoring genotypes with respect to RWC, LWP, TRL and RDW were identified and crosses made between them in genetic studies.

Results indicated significant genotypic differences in all the parameters. Water stressed plants maintained lower RWC and LWP than non-stressed plants. They also manifested faster growth in root length but had lower root dry weights than the non-stressed plants. Water stressed plants also flowered in shorter period than non-stressed plants. Significant positive correlations were observed between LWP and RWC as well as TRL and RGR.

Genetic studies showed that RWC was predominantly influenced by additive (d) and additive x dominance (j) genetic effects. Additive x dominance (j) genetic effects were predominant in taproot length while additive (d) and additive x dominance (j) genetic effects influenced root dry weight. LWP was largely controlled by additive (d) genetic effects. These results indicate that there is a genetic pool of variation in terms of the measured parameters which can be exploited in bean improvement for adaptation to semi-arid areas. The genetic effects imply that selection procedures that exploit epistatic genetic effects may be used in improvement programmes which target RWC and root growth as selection indicators. Delayed selection of these parameters beyond F_3 and later generations and then using bulk-pedigree breeding method

is suggested. On the other hand, high LWP would be best selected for by using pedigree and backcross breeding methods.

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W.K.A.R

1999

CHAPTER I

1.0 INTRODUCTION

1.1 Status of dry bean production in Kenya

Kenya's economy is largely dependent on the agricultural sector. This sector supports the majority of small holder resource-poor rural farmers who represent over 80% of the country's population. In addition, it contributes over 25% of the country's gross domestic product (GDP) and provides employment to about 20% of the population (CBS, 1997).

Much of the country's productive agriculture is confined to zones with high agricultural potential (800 - 1600mm of rainfall per annum). These areas are limited and are found in small pockets of the seven provinces (Rift valley, Nyanza, Western, Central, Eastern, Nairobi and Coast). Over the years, they have become highly populated. Well-established high-income generating crops like tea and coffee, and high-income livestock enterprise for example dairy farming are also concentrated in these areas. With the increase in population, there has been a trend for farming communities to migrate to the semi-arid areas (zones IV and V) to acquire land for agricultural production. The areas occupy over 60% of the total land mass and are found in Machakos, Makueni, Kitui, Mwingi, Isiolo part of Embu, Meru and Marsabit districts of eastern province. Kajiado, Narok, Bomet, Baringo, Nakuru, Samburu, West Pokot, Turkana and Laikipia districts of Rift Valley province; Homa bay, Siaya, Kisumu and Bondo districts of Nyanza Province; Busia district of Western province; parts of Kiambu, Thika Muranga, Nyeri and Nyandarua districts of central province; Kwale, and Kilifi, Lamu, Tana River and Taita Taveta districts of coast province (Fig. 1). These areas are largely characterised by low erratic and unreliable rainfall often of brief rainy seasons with extreme

variations in both the seasonal and annual amounts. This often leads to brief or extended droughts. The average rainfall ranges between 450 and 900mm per year (Braun, 1982). In Eastern semiarid areas of Kenya, the rainfall is bimodal and distributed with about equal amounts in each season. The two distinct rainy seasons are the so-called 'long rains' (March - June) and 'short rains' (October - January), peaking in 'April and November, respectively. These terminologies (long and short) refer to the length of growing seasons in western and central Kenya, where the long rains is associated with the main growing season (March – August). The 'short rains' are however more reliable than the 'long rains' in Eastern Kenya compared with the 'long rains'. Between the long and short rains, there is a distinct dry period. There is a great variation in the rainfall among years and months and even with the long rainy seasons. The onset of the rains and number of rainy days also vary. Common is also a dry spell of 10 - 15 days that occurs after the onset of rains (Dennet *et al.*, 1981). These conditions have direct influence on determination of date of planting, crop establishment and final plant population.

Dry bean is believed to have been cultivated in East Africa for over 300 years although no written records are available (Leakey, 1970; Mukunya and Keya, 1975). The wealth of local names given to different bean types in Kenya and Uganda is evidence of its long establishment as a cultivated crop. Although Kenya is the largest single producer of dry bean (*Phaseolus vulgaris* L.) in Africa and accounts for 25.8% of total production (Allen *et al.*, 1989), its hectarage yields are still low. The principal factors responsible for bean yield and quality losses are diseases, insect pests, plant nutritional deficiencies, drought and unreliable weather conditions (Nickel, 1989). A report by Kangethe and Ngalyuka (1989) indicates that

Eastern Province alone produces over 130,000 metric tons per season. This constitutes about 35% of Kenya's total production (Table 1). Although the area under production may not vary much from season to season and year to year, production per unit area varies from season to season and year to year (Table 2). This variation is mostly attributed to inadequate soil moisture during the growing season. Dry bean is grown usually in association with maize, sorghum, young fruit trees, vegetables and other pulses. A survey by Njuguna *et al.*, (1981) between 1974 and 1975 in Kenya indicated that 94% of the area planted with bean was in association with other crops while 6% was in pure stand. Another survey in lowland Machakos by Rukandema *et al.*, (1981) for two seasons reported 91% of the farmers grew their food crops in mixtures. The main crop mixtures during both seasons were maize, pigeonpea, cowpea and beans covering up to 80% of the available land. A related survey carried out between 1986 and 1988 in Machakos, Makueni, Kitui and Mwingi districts, established that various maize intercrops are practised (Table 3).

Dry bean is usually consumed in dry and green forms. The green form is consumed in limited quantities only when the crop has just attained physiological maturity or in the absence of other common vegetables. Bean and maize grains are mixed together to prepare *nyooyo* or *githeri* and *isyo* or dehulled maize may be mixed with beans to prepare *muthokoi*. Fried beans may be mixed with meat or green vegetables and eaten as a relish with *ugali, chapati,* rice or dehulled sorghum. Recently, new bean products such as bean *samozas*, and bean rolls have been developed at Katumani to enhance diversity in bean utilization (F. Kusewa and W.K. Ronno, unpublished). A part from being a relatively cheaper source of protein to resource

poor families, it forms a good source of income. Bean by-products are normally fed to livestock before returning to the farms in form of farmyard manure.

Drought stress often causes plant water deficits that reduce cell turgor and cell enlargement, closure of the stomata, reduction in leaf surface area and photosynthesis. Severe water deficit often result in further reduction of the rate of photosynthesis per unit leaf area and other plant physiological and metabolic processes (Begg and Turner, 1983, Kramer, 1983).

Table 1. Area, production, yield and percent of total production of drybean per province in Kenya (1986 – 1988).

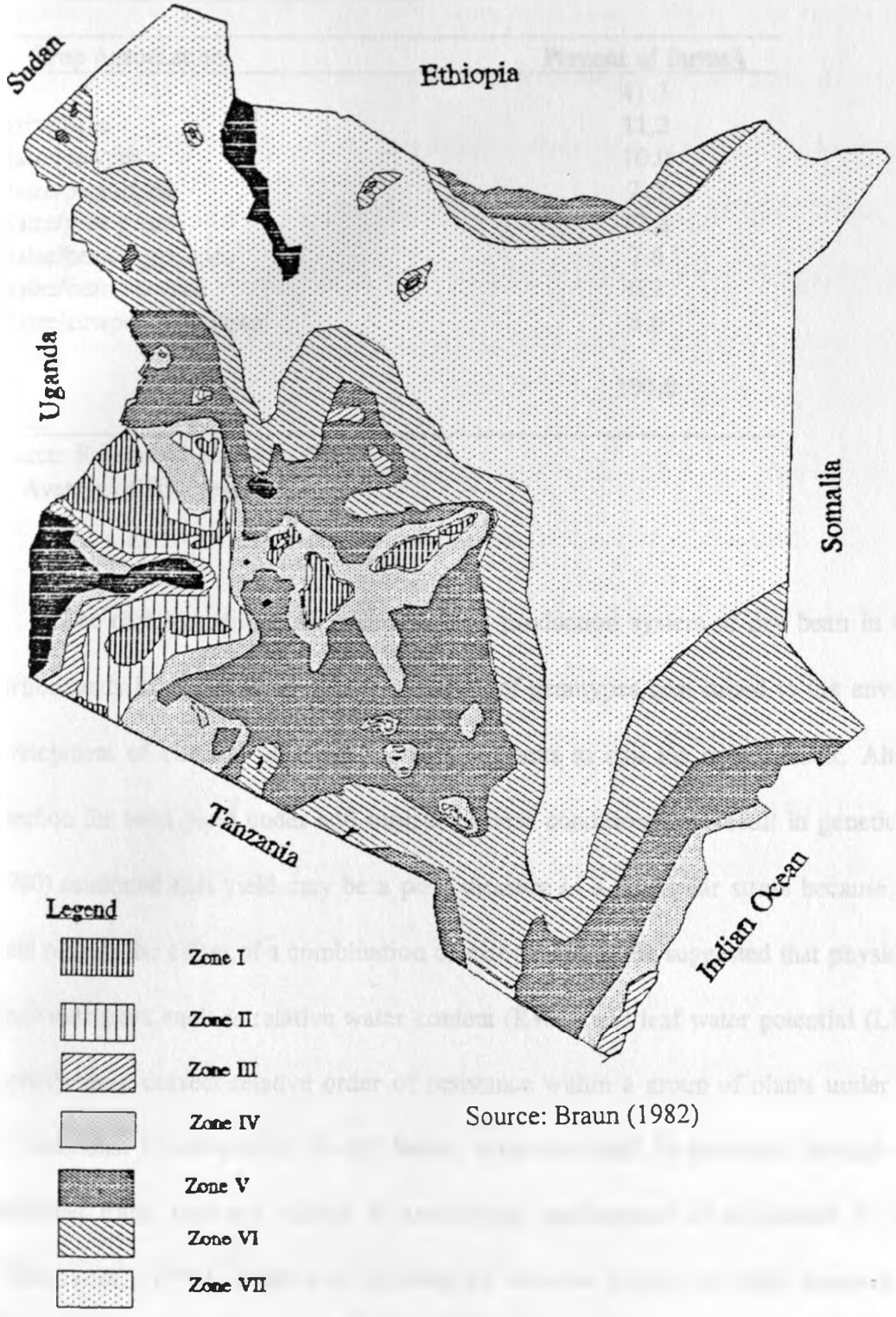
Province	Area (ha)	Production (tons)	Yield (Kg/ha)	% Production
Eastern	178,896	131,488	735	34.8
Rift Valley	120,782	89,131	738	23.5
Western	90,106	50,639	562	13.4
Central	86,166	54,198	629	14.3
Nyanza	61,065	50.806	832	13.4
Coast	3,412	2,156	632	0.6
Total	540,427	378,418	700	100

Source: Kang'ethe and Ngalyuka (1989)

Table 2. Area, production and yield of drybean in Eastern Province per district in 1990 and 1991

District	Area (ha)		Production (tons)		Mean yield (Kg ha^{-1})	
	Year					
	1990	1991	1990	1991	1990	1991
Machakos	100,346	111,543	79,455	60,233	792	540
Meru	49,864	54,908	4,021	29,642	806	540
Embu	27,805	29,870	22,244	20,202	630	361
Marsabit	3,370	1,490	1,800	800	534	537
Isiolo	84	35	44	63	523	1,800
Total	207,815	226,086	124,161	121,550	597	537

Source: Ministry of Agriculture, Annual Report 1991



Source: Braun (1982)

Figure 1. The Agro-ecological Zones of Kenya

Table 3. Mean Percentages of different crop combinations with maize in Matiliku, Machakos District (1986-1988).

Crop Association	Percent of farms§
	41.3
Maize/bean	11.2
Maize/cowpea	10.0
Maize/pigeonpea	2.5
Maize/gree gram	12.5
Maize/bean/pigeonpea	7.6
Maize/bean/cowpea	6.3
Maize/cowpea/pigeonpea	8.6
Others	
Total	100.0

Source: Ronno and Shakoor, 1990
§, Average of five seasons

The development of an optimum crop production system of dry bean in the semi-arid environments involves breeding and selection of genotypes best suited to the environment and development of cultural practices to manage plants to suit the environment. Although direct selection for seed yield under soil moisture stress conditions can result in genetic gain, Levitt (1980) cautioned that yield may be a poor measure of a particular stress because, in the field, yield reflects the effect of a combination of many factors. He suggested that physiological plant stress indicators such as relative water content (RWC) and leaf water potential (LWP), give an approximately correct relative order of resistance within a group of plants under a similar set of conditions. Consequently, in dry beans, progress could be enhanced through selection for additional traits that are related to underlying mechanisms of adaptation to water deficit (White, *et al.*, 1994). Success in breeding for varieties adapted to water stressed environment has been achieved by breeding for early maturity varieties, utilising drought escape

mechanism. Although these varieties are low yielding during seasons with favourable amounts of rainfall, yield stability is high. Dry bean varieties developed based on the mechanism of drought tolerance with high or low plant water potential *per se*, are however limited yet given the unpredictability of drought in each season in semi-arid tropics, even the drought escaping varieties need to have good drought tolerance properties to get them through mid-season drought episodes. Some of the varieties that have been developed in Kenya and other countries for cultivation under drought stress condition with possible drought tolerant mechanisms are presented in Table 4.

Identification of parents with desirable morphological and physiological traits, and selection for these traits in their progenies, might result in rapid progress. Rose *et al.*, (1992) using this line of approach found delayed senescence on soybeans based on a stress index to be a heritable trait even though this trait was not correlated with maturity. They therefore concluded that this source of tolerance to stress when used in conjunction with early maturity may provide an additional trait for improving soybean tolerance to moisture stress.

In Eastern semi-arid areas of Kenya where rainfall is limited and distribution is erratic, successful genotypes need rapid seedling emergence, high seedling vigour, and rapid crop establishment. These genotypes will be able to rapidly establish long and extensive root systems that can tap water below the dry upper soil layers. In addition, genotypes with high dehydration tolerance mechanisms can contribute to better performance in water stress environments as they would have enhanced ability to go through mid-season drought spells. Identification of genetic variability and selection of genotypes with long and extensive root systems and the understanding of the genetic control of these traits has not been adequately

studied. Part of the reason is in the difficulty to measure roots *in situ*. Similarly, information on the inheritance of these drought traits is limited.

Table 4. Some varieties developed for drought resistance in Kenya and other countries

Variety	Resistance mechanism	Country	Selected reference
GLP 1004, (Mwezi Moja)	Drought escape	Kenya	Njugunah, *et al.*, 1981
GLP x 92 Mwitemania	Drought escape and Drought avoidance	Kenya	Njugunah, *et al.*, 1981
Kat B1	Drought escape and Drought tolerance	Kenya	Muigai and Ronno, 1991
Kat B9	Drought escape and Drought avoidance	Kenya	Muigai and Ronno, 1991
BAT 477	Drought escape and Drought avoidance	Columbia	White and Izquierdo, 1991 Guimeraes, 1986
G5059	Drought escape and Drought avoidance	Columbia and Brazil	White and Izquierdo, 1991
Carioca	Drought escape and Drought avoidance	Brazil	Guimeraes, 1986
Black Ressie	Drought escape and Drought avoidance	Ethiopia	IAR, 1976
Tengeru 16	Drought escape and Drought avoidance	Ethiopia and Tanzania	IAR, 1976
A-211	Drought escape	Chile	Jara and Celis, 1989
Bukoba Coroli Kahawia	Drought avoidance	Tanzania	Kapuya, 1985

1.2 General objective

To identify physiological indicators of drought resistance that may be used to enhance dry bean improvement for semi-arid areas of Kenya.

1.2.1 Specific objectives

1. To determine genotypic differences in plant water status and growth of dry bean genotypes under different water regimes.
2. To study the interrelationships among the measured indicators of water status and growth in the dry beans.
3. To evaluate the genetic effects of relative water content (RWC), leaf water potential (LWP), taproot length (TRL) and root dry weight (RDW) as indicators of drought resistance.

1.2.2 Justification

The rapid increase in Kenya's population has created a trend for the farming communities to migrate to the semi-arid areas (agro-ecozones IV and V). These areas occupy over 60 % of Kenya's land mass and are characterised by low erratic and unreliable rainfall. The rains are unpredictable in terms of seasonal and annual amounts, onset, continuity and distribution so that the areas are prone to early season, mid-season and end-season drought episodes. These conditions have direct influence on determination of date of planting, crop establishment, final plant population and yield.

Although Kenya is the biggest single producer of dry beans in Africa, its hectarage yields are still low (Allen *et al.*, 1989). This was mainly attributed to adverse soil moisture

conditions (Halterlein, 1983) prevalent in Kenya's bean growing regions particularly if it occurs before full pod development.

To develop an optimum bean production system for semi-arid areas, breeding and selection of drought resistant genotypes and development of cultural practices to manage the crop to suit the environment is essential. Although direct selection for seed yield under soil moisture stress can result in genetic gain, yield alone may be a poor measure of a particular stress because in the field, yield reflects the effect of a combination of many factors. Some success in breeding for varieties adapted to water stressed environment has been achieved by breeding for early maturity utilising drought escape mechanism. Selection for this earliness in maturity however, assumes a condition of end season drought preceded by availability of rains early in the season and may not cater for mid-season drought so prevalent in tropical semi-arid areas.

There is need therefore to incorporate other mechanisms of drought tolerance in dry bean varieties for adaptation to these areas, even as an addition to early maturity to enhance and stabilise yields. An understanding and use of basic physiological drought resistance mechanisms in dry beans should hasten this process.

CHAPTER II

2.0 REVIEW OF LITERATURE

2.1.Drought and its effects on dry beans

Drought was defined by May and Milthorpe (1962) as a meteorological and environmental event, which is caused by the absence of rainfall for a period long enough to cause depletion of soil moisture and damage to plants. Drought stresses affect physiological and biochemical processes that in turn affect photochemical and photosynthetic activities of the plant and consequently agronomic traits. Plant damage is therefore a consequence of a disturbance of these various processes. Drought effects however vary greatly depending on specific drought conditions, crop species and phenological stage of the crop.

The yield and quality of dry beans is sensitive to soil water supply such that even brief periods of water deficits may adversely decrease growth (Halterlein, 1983). To function normally, living cells need to be more or less saturated with water, a condition that is usually not attained (Turner, 1979). It is generally agreed that the ultimate effect of drought is limitation of growth and yield. However, specific physiological effects of water stress vary depending on the previous history of the crop (for example, possible acclimation), timing and intensity of the stress, genotypes and the growth stage of the bean crop (White and Izquierdo, 1991). Interactions of such factors probably explain a large number of conflicting results from studies on drought effects (Kramer, 1983).

2.1.1 Plant water status

Two basic parameters commonly used to describe the degree of plant water deficit are relative water content (RWC) and the total water potential or leaf water potential (LWP). Field measurements of RWC and LWP show how far the internal water status is kept above the critical point during drought.The two parameters are linked such that the LWP decreases as the RWC decreases, a relationship variously known as the moisture release curve, water potential isotherm or water retention characteristic. This relationship varies with species, growth conditions and stress history (Turner, 1979). These parameters have gained prominence as measurements of plant water status under drought stress. Total water potential (Ψ) at any point in a plant can be partitioned into osmotic potential (π), turgor pressure (ρ), matric potential (τ) and gravitational potential. Gravitational component is very small and negligible in a short crop such as dry beans, but not in very tall trees (Connor *et al.*, 1977). For cells in equilibrium with their surroundings, ideally the total water potential is the same throughout the system i.e. in the wall cytoplasm, organelles and vacuoles (Turner, 1979). Jones, (1992); and Fontes and Pereira, (1994) suggested that predawn LWP values correspond to water potential approaching equilibrium between the plant and soil, while the midday LWP represented the minimum value for the water potential during the day. Drought adapted cultivars of Winter Wheat (Schonfield *et al.*, 1988), soybean (Sloane *et al.*, 1990) and dry beans (Runkulatile *et al.*, 1993) have been observed to maintain higher RWC values under water stress compared to less adapted ones.

Effects of desiccation due to drought may be grouped into (i) those that affect function of the cell membrane and (ii) those that effect protein function (Leopold *et al.*, 1981). The cell membranes affected by desiccation tend to lose integrity, and hence the efficiency of processes requiring membranes is reduced. However, evidence of effect of desiccation on enzymatic proteins has not been reported in beans.

2.1.2 Growth Rate

Growth analysis studies have proven to be useful in describing differences in crop species and varietal responses to environment (White and Izquierdo, 1991). Leaf area development and relative growth rate (RGR) are sensitive to mild water stress. With prolonged water stress, leaf area is reduced both through growth retardation, accelerated leaf senescence and shedding (Blum 1988; Ouma, 1988). RGR describes the rate of dry weight accumulated per unit of initial dry weight in terms of a compound interest law (Beadle *et al.*, 1985). In beans, under field water stress, high stomatal resistance, resulting in reduced transpiration has been associated with reduced RGR in cultivars Bayos Titan, BAT-240 and Bico de Ouro (Bascur, 1981) while a significant reduction in total leaf area was observed in cultivars Oregon 1604 and Galamor (Bonanno and Mack, 1983). Low RGR under water stressed conditions in these genotypes was due to reduced cell elongation arising from reduced turgor in the cells.

2.1.3 Photosynthesis and translocation of assimilates

The effect of water stress on photosynthesis via stomatal and non-stomatal factors has been demonstrated in beans (Bonanno and Mack, 1983; Markhart III, 1985; Ouma; 1988). Initial reduction in photosynthesis is usually due to stomatal closure and reduction in transpiration, resulting in parallel decline in photosynthesis. Non stomatal factors that are affected by stress that limit photosynthesis are chloroplasts and photochemical activities. Begg and Turner (1983) concluded that initial decline in photosynthesis is a result of stomatal closure, but with prolonged and severe water stress, chloroplast, photochemical and enzyme activities are depressed.

Omanya *et al.*, (1996) found that photosynthesis continued under drought in sorghum lines with higher leaf relative water content and stomatal conductance values, and hence suffered relatively less reduction in biomass and seed yield. Translocation of assimilates has been found to be less sensitive to water stress than is photosynthesis (Parsons, 1982). Water stress reduces the rate of assimilate movement from the photosynthetic cells into the conducting system and consequently into the sink. Begg and Turner (1983) concluded that reduced translocation caused by water stress is due to a direct effect on photosynthesis and assimilate loading at the source and not due to effects on the conducting system. The distribution of assimilate is therefore altered such that it accumulates in the leaves and reproductive structures at the expense of the roots and the stems. Induced or accelerated remobilization of stored dry matter caused by water stress has been observed in dry beans (Guimaraes *et al.*,1996). White and Izquierdo (1991) also clearly demonstrated that dry bean

genotypes that accumulated stem dry matter under stress conditions tended to show reduced yields. These observations are in agreement with Samper's (1984) studies in beans. He found that carbohydrate remobilization under drought conditions was more efficient in cultivars that are tolerant to drought during pod filling. ABA accumulation under the effect of stress is effective in inducing mobilisation of assimilates.

2.1.4 Proline and abscisic acid (ABA) accumulation

Proline in dry beans accumulates under drought stress conditions (Stewart, 1972). In sorghum, proline accumulation was related to the ability to recover after water stress and then irrigation (Blum and Ebercon, 1976). High proline accumulation in leaves of water stressed plants was suggested to be an adaptive response to drought for sorghum but not for beans (Al-Karaki *et al.*, 1995). Abscisic acid (ABA) phytohormone levels also increase under drought and can trigger the closure of the stomata (Aspinall, 1980). However, stomatal closure in beans was detected well before ABA increased (Walton *et al.*, 1977).

2.2 Drought Resistance in Dry beans

Drought resistance described as the adaptations to which plants survive in regions subject to drought, have been classified into three components by Levitt, (1972): drought escape, drought avoidance and drought tolerance. Various discussions have since then followed on the correct classifications (Jones *et al.*, 1981; Kramer, 1983). Whereas there are

no conflicting definitions to drought escape, there are general conflicting descriptions for drought avoidance and tolerance.

2.2.1 Drought escape

White and Castillo (1988) described two mechanisms of drought escape. The conventional one is simply that a genotype grows when soil moisture is still adequate, and matures before stress becomes severe. This was also indicated by Jones *et al.*, (1981) as characteristic of plants growing in areas possessing well-defined wet and dry conditions. Drought escaping plants therefore, complete their life cycle or at least their reproductive cycle before the soil moisture is depleted. Drought escape is usually related to earliness in maturity. The second alternative is that although a genotype shows normal maturity under irrigated conditions, its maturity date shows plasticity such that drought causes greater acceleration of maturity than occurs in other genotypes. Earliness in flowering and maturity are usually considered as effective drought escape mechanisms resulting in better seed yields in water stressed environments (White and Singh, 1991). Breeding for early flowering as a drought escape mechanism, was recommended as the most promising strtegy for arid and semi-arid zones by Fischer and Turner (1978).

2.2.2 Dehydration tolerance with high water potential

This phenomenon has been characterised as the ability of a plant to endure periods of water deficit while maintaining a high tissue water potential. Kramer (1983) described this to occur by physiological or morphological modifications that, maintain water uptake, for

example greater root growth and increased hydraulic conductance or modifications that causes reduction in water loss, for example reduced areas of evaporation and greater resistance along pathway of water loss (stoma).

2.2.2.1 Stomatal control

Stomata often close in leaves of plants sensitive to water deficit, leading to a reduction in transpiration under water stressed conditions. The absolute value of water potential that induces stomatal closure in beans varies with leaf age, leaf position, previous exposure of a plant to water stress and atmospheric conditions. Reduced transpiration is generally opposed to the maintenance of high yield potential due to a reduction in CO_2 diffusion into leaf thereby reducing photosynthesis (Jones, 1979). Based on these observations, Blum (1988) suggested selection of attributes that sustain optimum plant water status for maintenance of a high yield, without the expense of stomatal closure. In dry bean, genotypes with higher stomatal conductance values had inherently superior abilities to maintain open stomates under drought and hence better yield performance than others (Korir, 1996) probably due to a gradual closure of the stomates over a wide range of water potentials (insensitive genotypes). It has been suggested that screening genotypes for differences in stomatal characters such as size and frequency of stomata per unit leaf area, stomatal conductance and behaviour has much potential for future plant improvement (Jones, 1979). These characters are however not reliable. For example, stomatal closure under a mild reversible stress was found to cause a decline of net CO_2 uptake of a leaf (Cornie and Briantais, 1991). The internal leaf CO_2 concentration varied

during the dehydration stages of a leaf. They concluded that internal CO_2 concentration parameter, as a measure of drought tolerance was not adequate. Masumba (1984) and Markhart III (1985) found a consistent relationship between low values of stomatal conductance and transpiration rates in drought tolerant tepary bean.

The hydraulic permeability of the cuticle is fully determined by the cuticular resistance as well as by the epidermal waxes deposited over the cuticle (Blum, 1988). Further, conditions of water stress, high temperature and high radiation increases the density of wax embedded in the cuticle matrix of a leaf (Jordan *et al.*, 1983). These attributes would only be advantageous if tight stomatal closure occurred in the species during stress (Parsons, 1982). Anderson *et al.* (1984) found an increase by drought of 10-20 fold of phytol which is bound as wax ester in mature bean leaves. The wax was higher in drought resistant tepary than in the less resistant bean. Leaf pubescence also affect the spectral and aerodynamic characteristics of the leaves. In soybean, high pubescence was found to contribute to a reduction in leaf temperature and/or reduced transpiration (Baldocchi *et al*, 1983).

2.2.2.2 Intercepted solar radiation.

Plant water loss is reduced is by low interception of the solar radiation through leaf shedding (senescence) or the production of less leaf area, resulting in a reduced leaf area index (Blum, 1988) and loss in yield. For example, in soybean, De Souza *et al.*, (1997) found that moisture stress at seed filling, reduced yield by accelerating senescence and shortening the seed

filling period. Leaf hairiness or pubescence and epicuticular wax on the leaves and stem also increases reflectance of solar energy which reduces water loss (Turner, 1979).

Another method of reducing radiative load on the leaves is through perpendicular leaf orientation to incident solar radiation, often known as paraheliotropic leaf movement in water stressed dry beans and the drought tolerant tepary bean (Parsons, 1982)

2.2.2.3 Root development

An increase in root/shoot ratio is an important morphological adaptation to water stress that meet transpiration demand. An increase in root weight may indicate a greater density of roots or a greater depth of the roots (Turner, 1979); both are important morphological adaptations to water deficits in beans that enable a greater degree of extraction of soil water (White and Izquierdo, 1991). For example, drought tolerance has been found to be due to maintenance of high plant water status by deep roots and water retention in the plant (Guimeraes, 1986).

Drought tolerance arising from deeper root penetration under water stressed conditions has been demonstrated in bean varieties BAT 477 and Carioca (Guimaraes, 1986), Ulonzo, White Haricot, and GLP1004 (Runkulatile *et al.*, 1993); in beans and sorghum (Al-Karaki *et al.*, 1995); sorghum (Blum, 1979; Omanya *et al.*, 1996) and tepary bean (Markhart III, 1985). Greater root proliferation would also allow a greater soil volume exploration and this would allow the plant to survive under conditions of soil water deficits (Parsons, 1982). For example, in maize, development of highly branched root system which is large in relation to the shoot

may ensure adequate supply of moisture to enable genotypes to realise their inherent yield potential (Richner *et al.*, 1997).

In addition to large root systems, plants must also have low root resistances to water flow between the root and leaf (Hale and Orcutt, 1987; White and Izquierdo, 1991). This can be achieved by increasing the number of xylem vessels, without increasing their diameters (Turner, 1979).

2.2.3 Dehydration tolerance with low water potential in dry beans

Drought tolerance at low water potentials involve those mechanisms that enable a plant to adapt to low water potentials and maintain the processes inlvolved in growth, development and production (maintenance of turgor), and those processes that enable the protoplasm to survive and recover from severe water deficits (Turner, 1979; Morgan, 1980a; Blum, 1988). The maintenance of turgor as water potentials decrease is an important adaptation to water deficits. This adaptation may occur through changes in osmotic potential (Jones *et al.*, 1981, Morgan, 1984) or through an increase in cell elasticity (Turner, 1979).

2.2.3.1 Osmotic adjustment.

Osmotic adjustment occurs through physiological or metabolic processes that maintain turgor pressure. Turgor is essential for cell enlargement and growth and can be maintained by increasing osmotic concentration. Plant cells accumulate solutes which lower osmotic potential which may be regulated through shifts in concentrations of potassium, sugars, amino acids, and organic acids (Turner and Jones, 1980; Morgan, 1980a; Morgan, 1984).

Osmotic adjustment in response to drought stress is one of the most widely observed adaptive mechanisms of plants (Turner and Jones, 1980). Morgan (1984), has shown osmotic adjustment to be an important mechanism of drought resistance (drought tolerance with low water potential) through maintenance of turgor, leading to extension of the physiologically active range of water status in the leaves. This phenomenon has been observed in various crop species. For example, in *Phaseolus* species, peas and faba beans (Wood and Goldsbrough, 1997). Genotypic variations in osmotic adjustment appear to exist also among cultivars. For example, genotypic differences have been reported in sorghum, (Morgan, 1980a; Omanya *et al.*, 1996), wheat (Morgan, 1980a) and in chickpea, lentils, faba beans, field peas, grass peas and lupins (Turner *et al.*, 1996). In dry beans, genotypic variations have been reported. For example, Aduol (1993) observed that drought resistant bean cultivars maintained a fairly constant RWC over a wide range of decreasing LWP compared to the drought susceptible cultivars. She attributed this to be the ability of the cultivars to effect osmoregulation under water stress. Under field conditions, Jara and Celis (cited by White and Izquierdo, 1991) found significant differences in osmotic potential of about 0.05 MPa between two cultivars at the time of flowering. Drought tolerance by bean cultivar Durango-222 was attributed to a decrease in osmotic potential by an average of -0.125 MPa, as a result of osmotic adjustment (Padilla, 1989).

Although the responsible compounds that accumulate during osmotic adjustment are generally unknown, (Begg and Turner, 1983; Wood and Goldsborough, 1997) soluble solids have been reported to increase under stress in the young leaves of dry bean and tepary bean (Coyne and Serrano, 1983). Percentage soluble solids were higher in the drought tolerant bean

variety Pinto and tepary bean than in the susceptible ones. Other osmotic adjusting agents in the more drought resistant peas are sugars and amino acids (Wood and Goldsborough, 1997), proline in wheat (Munns *et al.*, 1979), potassium, salts of organic acids, and sugars in glycophytes (Begg and Turner, 1983). Age and reproductive stage of the plant may also affect the degree of osmotic adjustment. However, Korte *et al.*, (1983) suggested that the ability of a cultivar to adjust osmotically would be most important in the adult stages, since yield is most critically influenced by drought stress during the flowering and pod fill stage.

2.2.3.2 Cell elasticity

The second method through which plants maintain turgor is through an increase in cell elasticity. This parameter can be measured by resonance techniques or from the relationship between turgor pressure and cell volume, called modulus of elasticity (ME). Cell elasticity is influenced by osmotic potential, cell size or cell volume, cell wall structure and cell wall thickness (Hale and Orcutt, 1987). Smaller cells are more tolerant to water stress than larger cells (Turner, 1979). Other factors include availability of plant sugars in the cells. For example,stem infusion of liquid sugars in a culture medium prevented dessication of maize pollen at low water potential (Boyle *et al.*, 1991). An increase in cell sugars may also increase osmotic potential, resulting in a small decrease in water content per unit reduction in water potential when the plant tissues are water stressed rather than cell elasticity alone. In short, the protoplasm will retain more water under stress conditions. This mechanism however, has not been reported to be of much value in dry beans. For example, Kim and Lee-Stadelmann (1984) did not detect differences in cell elasticity, as measured by ME, on the trifoliate of beans in

water stress and control conditions, while Jara and Celis (1989) found such differences although not significant under field conditions in four water regimes.

2.3 Drought Resistance Breeding and Inheritance in Dry beans

Identification of drought resistance traits in beans can be useful in breeding programmes if the traits are sufficiently variable among genotypes to permit improvement and if the heritability of traits is high enough that progress may be attained through selection. Daday *et al.*, (1973) suggested that the germplasm pool of most cultivated crops contains genes for drought resistance or tolerance and that selection over time and diverse environments under water stressed conditions has probably favoured the accumulation of drought resistance alleles. The initial material screened should preferably therefore, be from adapted material since plant introduction and cultivars from other areas may have high resistance values but poor adaptation to a new location.

Since populations from diverse selection environments have probably accumulated different resistant alleles, and perhaps different mechanisms, crosses of parental genotypes from varied sources may offer the greatest genetic variance for selection (Hurd, 1969). Success in breeding crops adapted to drought stressed environments has been achieved by breeding for earliness or drought escape (Ronno and Shakoor, 1990; Muigai and Ronno, 1991; White and Singh, 1991). Moss *et al.*, (1974) and Wein *et al.*, (1979) emphasised that selection criteria for improving plant performance for a drought stressed environment may involve choosing plant characters and selection of genotypes based on yield performance. White, *et al.*, (1994)

further indicated that although direct selection for seed yield under soil moisture stress conditions can result in genetic gains in common beans, progress could be enhanced through selection for additional traits that are related to underlying mechanisms of adaptation to water deficit. Hale and Orcutt (1987) however cautioned that yield was a poor measure of water stress because, in the field, yield reflects the effect of a combination of many factors. In addition, Jordan and Miller (1978) suggested identification of genetic sources with superior performance and then incorporation of the traits into cultivars having desirable agronomic characters

Wallace *et al.*, (1972) also reported that with the exception of a few monogenic traits influencing drought resistance characters, most drought resistance mechanisms are polygenic. The identification of specific drought resistant germplasm containing a high frequency of drought resistance and subsequent introgression of this resistance into adapted material has been suggested for sorghum (Blum, 1979).

An understanding of plant physiology is essential for the success of the breeding effort. Experimental techniques must be developed or those available modified to fit the large number of measurements required in a successful breeding programme (Quizenberry, 1982). Many component processes that appear to contribute to survival or productivity under water stress have been described, as may be seen in books edited by Mussel and Staples (1979); and Christiansen and Lewis (1982). Many screening tests have also been devised although notable examples of their effective use in breeding programmes for water stress is limited (Evans, 1984; White and Izquierdo, 1991).

Once genetic contrasts for field-tested drought resistance responses have been found then subsequent studies could lead to elucidation of the operative resistance mechanism. The development of a drought resistance index for cultivars based upon several drought responses would be useful in selecting parents that might combine different drought resistance mechanisms (Myers *et al.*, 1986). Some of the stress indices which have been suggested are (a) arithmetic mean: (drought yield + control yield) / 2 (b) geometric mean: (drought yield x control yield) / 2. (c) Response: (control yield - drought yield) / difference in water applied to control and stress plots. (d) Percent reduction: [1 - (drought yield/control yield)] x 100. (e) Fischer and Maurer stress index: [1- (drought yield / control yield)/(mean yield overall stress / mean yield overall control)].

Blum (1988) suggested three approaches to screening. (i) The assumption that cultivars that are high yielding under non stress environments will also be relatively high yielding under stress conditions.(ii) Screening under stress conditions and disregarding the yield potential under non-limiting environmental conditions. In essence, selection for genotypes that specifically yield better under stress conditions and (iii) the assumption that yield and water stress resistance are separate, heritable characters. In this approach, one morphological, physiological and or physical response that contribute to drought resistance are identified by screening under drought stress, they can then be bred into high yielding genotypes. This approach was simply referred to as physiogenetic approach by Quizenberry (1982).

In addition, Johnson (1980) described the following features as important prerequisites in developing breeding programmes for drought resistance: (i) Availability of a broad-based germplasm to be screened (ii) Evidence of genotypic variability for drought resistance and (iii)

Ability to evaluate morphological, physiological and/or physical responses to drought stress in a reasonable time period using small quantities of seed.

Although evidence for genetic variation in various components of dehydration avoidance is ample (Blum, 1988), studies of mode of inheritance of drought predictive characters are limited. The inheritance study of root length, root thickness, root number and root/shoot weight in an 8-parent diallel of rice grown in an acroponic culture (Blum, 1988) indicated long root and high root number to be contributed primarily by dominant alleles in one parent, and high root/shoot ratio controlled by either dominant or recessive alleles, depending on the parents. Additive and dominance effects were noted in all four traits and narrow sense heritabilities were moderate. Heterosis has been reported in sorghum for seminal root length, growth rate of crown-root axes, and the total length and volume of crown roots (Blum *et al.*, 1977). Heterosis in total root dry matter was however, noted only in some sorghum hybrids.

Morgan (1983) using a cross between high and low osmoregulating wheat varieties proposed simple inheritance. Roarke and Quizenberry (1977) using upland cotton F_1, F_2 and backcrosses concluded that diffusive resistance or stomatal conductance was associated with both additive and dominance genetic variance. The estimated narrow-sense heritability was 25%. High leaf diffusive resistance was found to be completely dominant in this cross. The genetics of epicuticular wax load as a factor involved in developing avoidance was investigated in several crop species (Blum, 1988). For example, presence of waxy bloom over leaves of sorghum was controlled by a single dominant gene (Bm) while "bloomlessness" was conditioned by two different loci, designated as Bm1 and Bm2. "Sparse bloom" was governed

by homozygous - recessive alleles at a minimum of three loci, designated as h1, h2 and h3. The "bloomless" and "Sparse bloom" genes segregate independently and their various combinations may result in variable levels of epicuticular wax load. In wheat, glaucousness may be affected by a series of allelic wax-producing genes and their inhibitors. These alleles are either dominant or recessive on the B or D genomes (Blum, 1988). These are W1, W2, W2a, W2b and W21.

The inheritance of drought resistance in two resistant snap bean accessions was studied by Bouwkamp and Summers (1982). Drought resistance was measured in terms of the ability to avoid flower abscission and sustain pod formation when plants grew in a dry soil under relatively hot green house conditions. They found that drought resistance was conditioned by a single dominant gene in one accession and by two genes with epistatic action in the other. Resistance of the two accessions could not be recombined into a higher level or resistance. It was not clear however whether the effects they measured could be ascribed to drought or heat stress. Proline accumulation *per se* may be inherited in a relatively simple manner as evidenced by isolation in barley of a proline accumulating mutant (Kueh *et al.*, 1984), which accumulated three to six fold more proline than the wild type, apparently in no relationship to the water status of the plant. Delayed senescence in soybean populations grown under terminal drought stress conditions is heritable (Rose *et al.*, 1992).

2.4 Some selection criteria for drought resistance

Dehydration avoidance, as an effective component of drought resistance can be evaluated under field stress conditions by using several indirect methods (Blum, 1988). Morphological, physiological, biochemical, cytological, ultra structural, and physical responses assumed to be inherent in drought resistance have been summarised in Table 5 (Myers *et al.*, 1986).

Table 5. **Some indicators and methods of detecting drought resistance.**

Indicators of Drought Resistance	Resistance Mechanism	Detection Method
a) Morphological		
1.Continued leaf expansion primary and second trifoliate at lowered soil water potential (SWP)	Drought avoidance and tolerance.	Determination of leaf area following mild and moderate drought stress; determination of leaf water potential (LWP) for 50% reduction.
2. Formation of rapidly growing deep and extensive roots system.	Drought avoidance	Determination of root length and volume under moderate drought stress.
b. Physiological		
1. Decreased Stomatal transpiration at critical SWP	Drought avoidance	Determination of SWP and LWP for 50% reduction of transpiration.
2. Capability to osmoregulate resulting in maintenance of turgor	Drought tolerance	Determination of SWP and LWP at decreasing relative water content (RWC).
3. Capability to be "hardened" to drought stress	Drought avoidance and tolerance	Subject plants to alternate drying and re-watering followed by subsequent testing of changes in morphological, physiological, biochemical and physical drought responses.
4. Response to applied ABA	Drought avoidance and tolerance	Determination of effect on membrane leakage.

Table 5 (continued

Biochemical		
1.Maintenance of high nitrate reductase activity (NRA) at lowered SWP.	Drought avoidance and tolerance	Determination of NRA in most recently expanded leaf at decreasing SWP and LWP at which NRA falls to 50% of unstressed level
2.Lack of proline synthesis and accumulation at lowered SWP	Drought avoidance and tolerance	Determination of SWP and LWP at which proline accumulation begins
d. **Cytological and ultrastructural**		
1. Maintenance of nuclear and nucleolar dry masses and areas at lowered SWP	Drought avoidance and tolerance	Determination of nuclear area and dry mass in epidermal cells from drought stressed plants.
e) **Physical**		
Maintenance of Membrane integrity (lack of leakiness) at lowered tissue WP	Drought tolerance	Determination of release of ultraviolet absorbing solutes (220 nm from leaf discs subjected to 50% fresh weight level.
f) **General**		
1. Possession of varying low critical WP for non recovery upon re-watering	Drought tolerance	Determination of RWC and or LWP below which plants will not recover
2. Maintenance of cotyledonary function at lowered SWP	Drought avoidance and tolerance	Determination of SWP which cotyledonary abscission begins

Source: Myers *et al.*, (1986).

CHAPTER III

3.0 MATERIALS AND METHODS

Three experiments were conducted to study physiological and morphological responses of dry beans to water stress and evaluate the genetic effects of some of these physiological and morphological parameters.

3.1. Experiment I: Effect of water stress on plant water status and growth of dry bean genotypes.

Thirty-six dry bean genotypes collected from various agro-ecological zones of Kenya and from Centro Internacional de Agricultura Tropical (CIAT) were planted in the field under two irrigation levels. The experiment that had two treatments (genotype and irrigation) was repeated over two seasons namely January - April 1996 (Season 1) and May - July 1996 (season 2). The bean genotypes included the bushy determinate (type I) and medium indeterminate (Type II) and were selected to include known drought resistant and non-drought resistant genotypes as checks (Table 6).

Two irrigation levels namely water stressed (WS) and non-stressed (NS) were imposed on the bean genotypes using an overhead sprinkler irrigation system. Pre-calibrated catch cans placed at canopy height were used to measure the amount of water applied at each irrigation. Studies on the same site have shown that at field capacity, (assumed to be at 100%) soil contains 33.7 mm while the potential evapotranspiration is estimated at about 5 mm day^{-1} (Shisanya, 1995). The area within the experimental plots was watered to field capacity (both WS and NS) with about 30 mm immediately after planting and a further 60 mm upto emergence to facilitate

uniform germination. Thereafter the NS treatment continued to be irrigated weekly for a period of 2 months at a rate that compensated the net deficit between evaporation (Pan) and rainfall in the preceding week. The WS treatment was not watered after the pre-emergence irrigation and only received moisture whenever there was rain or when minimal irrigation had to be applied to save the crop from desiccation. In total the WS treatment received 194.4 mm and 186.3 mm of precipitation in first and second seasons, respectively compared to 312.4 mm and 304.5 mm received by the NS plots in the first and second seasons, respectively.

The experiment was laid out in a split-plot design with irrigation treatments as the main plots and genotypes allocated to sub-plots. Each plot comprised 5 rows 3 m long. Plant spacing was 45 cm between rows and 15 cm within rows. There were two replicates. To avoid border effects from the different water regimes water applications, additional plots were planted between them but no measurements were made on them. Disease, insect pest and weed control measures were taken to give the crop the necessary protection during both seasons.

The experiments were conducted at the National Dryland Farming Research Centre's Kiboko sub-centre. The sub-centre is located at 975m asl and coordinates of 2° 12′ S and 37° 43′ E and about 160 km south east of Nairobi. The soils are classified under the Acrirhodic Ferralsols group and described as well drained, very deep, dark reddish brown to dark red, friable with high structural stability (Michieka and van der Pouw, 1977). The mean temperature at the centre was 25.5°C during the first season and 23°C during the second season. The study was conducted during dry season to allow for controlled water application with little interference from the rains. The following parameters were measured: Leaf relative water content (RWC), leaf water potential (LWP), relative growth rate (RGR), and days to flowering (DTF).

Table 6. **Identification, plant type, origin and agro-ecological zone (AEZ) from which the dry bean genotypes were collected for the studies on the drought traits at Kiboko.**

GENOTYPE IDENTIFICATION	GROWTH HABIT †	DISTRICT OF ORIGIN	PROVINCE/ COUNTRY	AEZ§
1	I	Machakos	Eastern	III
2	II	Kitui	Eastern	IV
3	II	Kisii	Nyanza (H)	II
4	II	Embu	Eastern (H)	III
5	I	Kakamega	Western	III
6	I	Kakamega	Western	III
7	II	Nyeri	Central	II
8	II	Kirinyaga	Central	II
9	I	Kitui	Eastern	IV
10	I	Nyeri	Central	II
11	II	Kisii	Nyanza (H)	II
Kat B9	I	Makueni	Eastern	V
GLP x 92	II	Machakos	Eastern	IV
GLP 1004	I	Machakos	Eastern	III
Okuodo	II	Kisumu	Nyanza	III
16	II	Kitui	Eastern	V
Kat B1	I	Makueni	Eastern	IV
GLP 2	I	Ex-kawanda	Uganda	II
19	II	Kakamega	Western	II
20	I	Nyeri	Central	II
21	I	Kiambu	Central	II
22	II	Taita	Coast	II
23	II	Meru	Eastern	III
24	I	Machakos	Eastern	IV
Mbalaria	II	Migori	Nyanza	II
26	II	Migori	Nyanza	II
27	II	Kwale	Coast	IV
28	I	Kisii	Nyanza (H)	II
SEQ 1001	II	CIAT	S. America	-
SEQ 1004	II	CIAT	S. America	-
SEQ 1008	II	CIAT	S. America	-
SEQ 1012	II	CIAT	S. America	-
SEQ 1014	II	CIAT	S. America	-
34	II	Kiambu	Central	II
Ulonzo	II	Kitui	Eastern	V
White Haricot	II	Taita	Coast	V

† Growth habit I = determinate, II = indeterminate

H = Highlands, § = Agroecological zone according to classification by Braun (1982)

3.1 (i) Leaf Relative Water Content (RWC)

Estimates of RWC were made between 0600 and 0730 h (predawn) and between 1200 and 1400 h (midday). Ten leaf discs, 7 mm in diameter were punched out from the recently most expanded leaf on each of the three plants selected in each plot. After weighing immediately using an electronic balance to determine fresh weight (FW), the discs were placed in a vial containing de-ionised water for 16hours at 5°C (Runkulantile *et al.*, 1993) in order to regain turgor. The discs were then removed from the vials, gently wiped using a blotting paper and then re-weighed to obtain turgid weights (TW). Each sample was again immediately replaced back in the empty vial and oven dried at 70°C for 48 hr. to obtain a constant dry weight (DW). Other procedures were followed as recommended by Turner (1979). The first estimate was done 15 days after emergence (DAE) and weekly thereafter for 3 weeks.

The estimate of leaf turgor in each sub-plot was calculated as follows: -

$$RWC = [(FW - DW)/(TW - DW)] \times 100$$

3.1 (ii) Leaf Water Potential (LWP)

To measure the LWP, a portable pressure chamber (model PMS Instrument Co.; Oregon, USA) was used as described by Turner (1979). Estimates of LWP were made between 0600 and 0730 h (predawn) and between 1200 and 1400 h (midday). A young fully expanded trifoliate leaf was cut quickly using a sharp razor blade, wrapped with a cling foil and placed in the chamber of the pressure bomb with cut end of the petiole just protruding from the chamber through a rubber plug which is used to seal the chamber. A moist paper cloth was placed inside the chamber to prevent water loss in the chamber itself. Pressure inside the chamber was gradually increased by

using compressed nitrogen gas from a cylinder until the sap exuded to the cut end of the xylem vessels. The operation generally took less than 2 minutes. The Detection of exudation of water at the end point was made using a hand lens. Three plants were sampled for measurement per plot. The readings were in bars but were converted to Mega Pascal (MPa) units (1 bar = 0.1 MPa). Measurements were made at pre-dawn and at midday during four episodes namely: 15, 22, 29 and 36 DAE.

3.1 (iii) Relative Growth Rate (RGR)

Two RGR values were determined between seedling (15 DAE) and pre-flowering (22 DAE); termed as RGR1 and between pre-flowering (22 DAE) and flowering (29 DAE) termed as RGR2 stages both under water stress and non-stress treatments. To obtain the RGR1 and RGR2 values, dry weight at seedling (15 DAE), pre-flowering (22 DAE) and flowering (29 DAE) were obtained by cutting the plants at the ground surface. Six plants were randomly selected in each plot. The plants were then oven-dried to a constant weight at 70^{o}C. The average value per plant represented the mean for each plot.

The RGR was calculated as:

$$RGR = \{(1/w) \times (\delta w/\delta t)\}$$

Where, w = average plot dry weight (g)

δw = change in dry weight (g)

δt = time between each harvest date (15 - 22 DAE and between 22 – 29 DAE)

3.1 (iv) Days to 50% Flowering (DTF)

This parameter was measured as the number of days from date of planting to date when 50% of the plants in each plot had one or more first flowers also known as developmental stage R6 (CIAT, 1987).

3.2 Experiment II: Effect of Water Stress on Root growth of Dry bean genotypes.

The 36 genotypes used in experiment I (section 3.1) were evaluated for taproot length (TRL) and root dry weight (RDW) under two water regimes in a trough experiment. Troughs constructed using baked bricks and located adjacent to plots of experiment I were filled with field soil. Four troughs were constructed. Each trough measured 10.8 m x 3.5 m of 1.2 m high. The experiment was designed as a split plot of three replicates with irrigation treatment allocated to the main plots and the genotypes to the sub-plots. In all the treatments, seeds were planted at 30cm between rows and 15cm within the rows. Each sub-plot was of one 1m row length. The experiment was repeated for two seasons. Appropriate fertility and crop protection methods were taken to maintain a healthy crop.

All troughs were fully irrigated to field capacity prior to planting using a 20-litre water bucket. The procedures for calculating the amount of water required per trough were adopted from Doorenbos and Pruitt (1977).

$Q\ (m^3) = 10/Ea\ (P \times Sa) \times D \times A$

Where Q = amount of irrigation required

Ea = application efficiency (assumed at 65%)

P = fraction of total available soil water permiting evapotranspiration

Sa = total available soil water

D = rooting depth (m)

A = trough size in hectares

No additional irrigation was applied to the water stressed treatment (WST). The non-stressed treatment (NST) was maintained at near field capacity throughout the experimental period by applying water after every 2 - 3 days.

Taproot length and root dry weight were monitored on two occassions namely 15 DAE and 36 DAE respresenting seedling and pod development stages, respectively. At each sampling date, troughs were well-watered about 6 hours prior to sampling to allow easy removal of the bricks without interfering with the roots. At sampling time the bricks bordering one side of each trough were carefully removed exposing the roots. Each plant was then carefully dug out and immersed in a container of water to soak and remove the soil surrounding the roots. Roots so washed were measured for length by using a ruler and subsequently severed at the stem base and oven dried to determine root weight. Six plants in each plot were harvested to obtain these measurements.

3.3 Statistical Analysis

All data for irrigation and non-irrigation treatments were subjected to analysis of variance using the general linear models (GLM) procedure of SAS (SAS Inst., 1988) and analysis of variance (ANOVA) following procedures described by Steel and Torrie (1980) as given in Table

7. Genotype means were separated by use of Duncan's Multiple Range Test (DMRT). A combined analysis of variance over irrigation treatments was carried out at each measuring episode (15, 22, 29 and 36 DAE) in each season.

Pearson correlation coefficients were evaluated using PROC CORR SAS statistical packages (SAS Inst. 1988) to determine the relationships among the drought resistance traits. The correlation coefficients were based on individual genotype means averaged over replications. The trough data was also analysed similarly.

Table 7. Analysis of variance per season per measuring episode.

Source	df	Expected mean squares (EMS)
Replication	(r-1)	
Irrigation	(i-1)	
Error (a)	(r-1)(I-1)	
Genotype (G)	(g-1)	$\sigma^2 + r\sigma_{GI} + ri\sigma^2_G$
Genotype x Irrigation	(g-1)(i-1)	$\sigma^2 + r\sigma_{GI}$
Error (b)	i(r-1)(g-1)	σ^2

3.4 Experiment III: Genetic analysis of indicators of plant water status and of root growth.

Based on the results of experiment I and II, contrasting parental lines were crossed for genetic analysis of the following perameters.

3.4.1 Relative Water Content (RWC)

Data from experiment I showed that genotype 4 (Ex-Embu) maintained consistently high RWC values under water stress. Conversely, genotypes 10 (Ex-Nyeri) and 28 (Ex-Kisii) maintained consistently low RWC values. Genotype 4 (Ex-Embu) was therefore crossed with these two other genotypes to generate F_1, F_2 and backcrosses of F_1 to each of the parents (Table 8). The parents and the crosses were planted in the field under water stressed conditions in which the plots were watered to field capacity at planting and maintained upto emergence, to facilitate uniform germination, following the methodology described in subsection 3.1 (i). Supplemental irrigation was only applied when severe water stress was observed. In cross P4 x P10, the population sizes were 27 plants per parent, 31 plants per F_1, 119 plants per F_2, 38 plants per BC_1 (F_1 x P4) and 43 plants per BC_2 (F_1 x P10). In cross (P4 x P28) populations sizes were 27 plants per parent, 32 plants per F_1, 108 plants per F_2 and 36 plants each for BC_1 (F_1 x P4) and BC_2 (F_1 x P28)

The experimental design was a randomised complete block of three replications. The RWC was monitored at two occassions namely 22 and 36 DAE in parents and their crosses following procedures described in subsection 3.1 (i).

3.4.2 Leaf Water Potential (LWP)

Data from experiment I also showed that genotypes 2 (Ex-Kitui) and 4 (Ex-Embu) maintained consistently high LWP values under water stress. Conversely, genotype 20 (Ex-Nyeri) consistently maintained low LWP value in both seasons. Genotypes 4 (Ex-Embu) and 2 (Ex-Kitui) were crossed with genotype 20 (Ex-Nyeri) to generate F_1, F_2 and backcrosses of F_1 to each of the parents (Table 8). The parents and the crosses were planted in the field under water stressed conditions in which the plots were watered to field capacity at planting and maintained upto emergence to facilitate uniform germination, following the procedures described in subsection 3.1 (ii). Minimal irrigation was only applied when severe water stress was observed. In cross P2 x P20, the sample sizes were 31 plants per parent, 35 plants per F_1, 103 plants per F_2, 42 plants per BC_1 (F_1, x P4) and 49 plants per BC_2 (F_1 x P10). In cross (P4 x P20) sample sizes were 39 plants per parent, 42 plants per F_1, 92 plants per F_2 and 46 plants each for BC_1 (F_1 x P4 and BC_2 (F_1 x P20).

The experimental design was a randomised complete block of three replications. The LWP was monitored at two occassions namely 22 and 36 DAE in parents and their crosses following the procedures described in subsection 3.1 (ii).

Table 8. **Cross combinations and the traits measured in the parents and their generations for determining genetic effects.**

Cross¶	**Traits measured**
4 x 10	Relative water content
4 x 28	Relative water content
2 x 4	Leaf water potential
2 x 20	Leaf water potential
2 x 8	Taproot length and Root dry weight
2 x 23	Taproot length and Root dry weight

¶The origin of the parents is indicated in Table 6.

3.4.3 Taproot length (TRL) and Root dry weight (RDW).

Results from experiment II showed that genotypes 2 (Ex-Kitui) and 8 (Ex-Kirinyaga) under water stress consistently had longer taproots and root dry weights, while genotype 23 (Ex-Meru) consistently had low values compared to other genotypes. Genotypes 2 (Ex-Kitui) and 8 (Ex-Kirinyaga) were crossed with genotype 23 (Ex-Meru) to generate F_1, F_2 and backcrosses of F_1 to each of the parents (Table 8). The parents and the crosses were planted in a trough in the field under water stressed conditions in which the plots were irrigated to field capacity at planting and maintained upto emergence to facilitate uniform germination, following the methodology described in subsection 3.2. No other irrigation was applied after germination. The sample sizes in cross (P2 x P23) were 25 plants per parent 27 plants per F_1, 98 plants per F_2, 59 plants each for BC_1 (F_1 x P2) and BC_2 (F_1 x P23). In cross (P8 x P23), the sample sizes were 25 plants per parent, 23 plants F_1, 90 plants per F_2, 53 plants for BC_1 (F_1 x P8) and 48 plants for BC_2 (F_1 xP 23).

The experimental design was a randomised complete block of three replications. TRL and RDW were measured at 36 DAE in parents and their generations following procedures described in subsection 3.2.

3.5 Genetic Analysis

Estimates of the genetic effects are obtained from unweighted least squares analysis of the generation means procedure (Mather and Jinks, 1977; Hayman, 1958 and by Rowe and Alexander, 1980). The parameters estimated by this analysis are **m**, mean of F2; **d**, pooled additive effects; and **h**, pooled dominance effects for a 3-parameter model for each cross by least squares. An F-test is used to determine adequacy of the model. A model is deemed inadequate when the mean square is not significant. The adequacy of these analyses is based on the following assumptions (Hayman, 1958; Mather and Jinks, 1977):

i. Families must be raised in comparable environments so that differences between their means are basically due to genotypic differences.

ii. Constant viability of all the genotypes included in the families raised or absence of mutations

iii. The two parents should be homozygous or highly inbred. The phenotypic departure of each of them from midparent reflects the simultaneous action of all the genes affecting the character by which the lines differ. This assumption is valid for self-pollinating crops, for example dry beans.

iv. Absence of genetic linkages or interactions between non-allelic genes. This assumption of absence of epistasis may not be realistic when dealing with quantitative traits such as yield.

v. Simple autosomal pattern of inheritance is assumed. Genes should not be sex-linked or maternally inherited.

vi. It is also assumed that lethal genes are absent.

The inadequacy of a 3 parameter model is was found, suggesting invalidity of the above assumptions (existence of linkages or higher order epistatic effects). A 6-parameter model was used following notations of Hayman (1958) and procedures described by Rowe and Alexander (1980). The parameters fitted by 6-parameter model analysis are **m,** mean of F2; d, pooled additive effects; **h,** pooled dominance effects; **i,** pooled interaction among additive x additive effects; **j**, pooled interaction among additive x dominance effects; and **l**, pooled interaction among dominance x dominance effects. Estimates of the d, h, i, j and l were calculated for each cross by using least squares. Expectations of generation means for each cross used for estimating genetic effects are presented in Table 9. The sum of squares attributable to each genetic effect was determined by fiting the 6-parameter model for each gene effect to the total sum of squares witin each cross. Matrix inversion was used to solve the equations. An F-test was used to determine significance of variation attributable to a specific gene effect. The model was corrected for the mean (**m**) effect and replication x generation mean square was used as an error term.

Percent genetic variability for each gene effect was calculated by using its mean square value and the total generations mean square, corrected for the mean (**m**) effect. By doing so,

the magnitude of the different genetic effects within and among the crossses and traits measured was easier to compare. The term 'percent of total genetic variability' was adopted to facilitate clarity. All statistical analyses were carried out using PROC GLM SAS routines.

Table 9. Expectations of generation means for each cross used for estimating gene effects in a 6-parameter model.

	GENETIC EFFECTS					
Generation	**m**	**d**	**h**	**i**	**j**	**l**
P_1	1	1	-½	1	-1	¼
P_2	1	-1	-½	1	1	¼
F_1	1	0	½	0	0	¼
F_2	1	0	0	0	0	0
$BC_1(F_1P_1)$	1	-½	0	¼	0	0
$BC_2(F_1P_2)$	1	½	0	¼	0	0

Where:

- P_1 = high value parent
- P_2 = low value parent
- F_1 = the first generation of a cross
- F_2 = the second filial generation obtained by self-fertilization
- BC_1 F_1 = the cross of the first generation of a cross (F_1) to the high value parent
- BC_2 F_1 = the cross of the first generation of a cross (F_1) to the low value parent
- m = mean of the F_2
- d = pooled additive effects
- h = pooled dominance effects
- i = pooled additive x additive interaction effects
- J = pooled additive x dominance interaction effects
- l = pooled dominance x dominance interaction effects

CHAPTER IV

4.0 RESULTS

4.1 Experiment I. Effects of water stress on plant water status and growth of dry bean genotypes

4.1.1 Relative Water Content (RWC)

In both seasons, the genotype x irrigation interaction effect was significant ($P<0.05$) at predawn and at ($P<0.01$) at midday during all the sampling episodes, except 15 DAE (Tables 10 and 11). Predawn RWC values were always higher than midday values. Both predawn and midday RWC values descreased as the season progressed from 15 DAE to 36 DAE (Tables 12 and 13).

Genotypic effects were also significant ($P<0.01$) during both seasons. For example, at predawn, under water stress treatment (WS) in the first season, the average RWC values varied from 69.8% to 95.8%, 66.6% to 90.3%, 59.0% to 88.8% and 58.4% to 83.2% on 15, 22, 29 and 36 DAE, respectively. Genotypes 2 (Ex-Kitui), 4 (Ex-Embu), GLP x 92 and Ulonzo consistently had high RWC values above 80% at all sampling episodes and above 85% at 15, 22 and 29 DAE. Conversely, genotypes 10 (Ex-Nyeri), 20 (Ex-Nyeri), 23 (Ex-Meru), 28 (Ex-Kisii), SEQ 1001 and SEQ 1012 had average RWC values which were consistently lower than 75% at all sampling espisodes. These genotypic differences were generally maintained even at midday in both seasons.

Table 10. Predawn and midday RWC mean squares from analysis of variance at 15, 22, 29 and 36 DAE during Jan – March 1996 (season 1) at Kiboko

Source of Variation	df	Predawn				Midday			
		15 DAE	22 DAE	29 DAE	36 DAE	15 DAE	22 DAE	29 DAE	36 DAE
Irrigation	1	4.5	62.9	65.3	43.2	48.2	93.1	41.2	30.2
Rep (Irrigation)	2	22.0	41.8	68.5	15.0	53.4	49.9	75.6	45.5
Error (a)	2								
Genotypes	35	80.8	111.4**	172.5*	241.5**	191.8*	205.7**	212.9**	311.8**
Genotype x Irrigation	35	12.2	65.6*	112.3**	133.5**	32.3*	132.6**	79.4**	271.7**
Error (b)	70	533.2	28.2	36.4	40.0	31.0	38.1	38.0	81.3
CV (%)		4.5	7.0	9.3	9.9	8.4	7.5	10.6	8.1

*, ** significant at P< 0.05 and 0.01 levels, respectively.

Table 11. Predawn and midday RWC mean squares from analysis of variance at 15, 22, 29 and 36 DAE during May - July 1996 (season 2) at Kiboko

Source of Variation	df	Predawn				Midday			
		15 DAE	22 DAE	29 DAE	36 DAE	15 DAE	22 DAE	29 DAE	36 DAE
Irrigation	1	934.7	615.5	156.9	445.6	843.4	434.8	236.9	112.2
Rep (Irrigation)	2	8.6	0.9	66.9	20.4	131.9	101.9	117.3	57.3
Error (a)	2								
Genotypes	35	128.1	276.2**	307.2**	241.5**	17.5	101.6**	257.5**	246.9**
Genotype x Irrigation	35	63.4	52.6*	73.2	154.7**	51.0	145.6**	59.4**	171.7**
Error (b)	70	533.2	28.2	36.4	40.0	31.0	38.1	38.0	81.3
CV (%)		9.3	6.4	8.0	8.3	7.4	8.3	9.1	12.5

*, ** significant at $P < 0.05$ and 0.01 levels, respectively.

Table 12. **Predawn and midday leaf relative water content (RWC) for 36 dry bean genotypes measured at four sampling episodes under field water stress and non-stress conditions during January - March 1996 (season 1) at Kiboko .**

	15 DAE						22 DAE					
Genotype	PS[1]		MS		MNS		PS		MS		MNS	
1	92.4	abc	77.0	b-g	91.5	a	88.0	abc	76.2	a-e	90.6	ab
2	91.9	abc	85.6	a-e	95.7	a	86.1	a-e	77.8	a-d	91.1	ab
3	81.1	b-l	89.9	a	92.5	a	80.9	a-h	77.2	a-d	89.6	ab
4	95.8	a	87.9	ab	92.6	a	90.3	a	84.5	a	87.2	ab
5	87.3	a-g	76.5	b-g	91.7	a	83.4	a-g	73.2	a-f	90.5	ab
6	84.2	a-i	68.5	gh	91.7	a	78.6	a-i	64.8	efg	90.1	ab
7	89.1	a-d	81.1	a-f	94.2	a	85.6	a-e	76.2	a-e	89.2	ab
8	93.2	ab	81.1	a-f	92.1	a	82.6	a-g	73.8	a-f	87.2	ab
9	79.3	d-l	77.7	b-g	91.3	a	71.9	ghi	75.5	a-f	89.0	ab
10	69.8	lk	62.5	h	89.8	a	66.6	i	59.8	g	80.1	b
11	81.8	b-l	83.1	a-f	90.7	a	80.9	a-h	79.3	ab	89.2	ab
KatB9	86.2	a-h	82.5	a-f	91.8	a	84.4	a-f	77.2	a-d	89.6	ab
GLPx92	89.9	a-d	87.2	abc	94.2	a	88.9	ab	78.5	abc	92.3	ab
GLP1004	75.8	g-l	80.1	a-g	95.6	a	72.1	ghi	70.1	c-g	88.2	ab
Okuodo	84.0	a-i	75.3	c-g	91.9	a	80.1	a-h	74.6	a-f	89.1	ab
16	84.7	a-i	75.5	c-g	90.3	a	78.1	b-i	72.3	b-f	88.4	ab
Kat B1	83.6	b-j	81.7	a-f	91.0	a	79.4	a-h	74.4	a-f	89.2	ab
GLP 2	76.3	f-l	77.3	b-g	93.4	a	66.7	i	74.6	a-f	85.7	ab
19	88.4	a-f	79.1	a-g	90.2	a	79.9	a-h	75.4	a-f	87.2	ab
20	74.9	h-l	81.5	a-f	93.3	a	71.5	ghi	63.7	fg	89.5	ab
21	80.5	c-l	77.6	b-g	90.2	a	77.4	b-i	73.0	a-f	88.8	ab
22	88.8	a-e	79.8	a-g	93.5	a	80.2	a-h	71.3	c-g	91.4	ab
23	73.3	i-l	73.8	e-g	90.2	a	69.7	hi	69.2	c-g	91.0	ab
24	80.4	c-l	79.6	a-g	95.6	a	79.4	a-h	76.6	a-e	91.2	ab
Mbalaria	86.5	a-h	75.5	c-g	89.7	a	75.4	d-i	74.3	a-f	89.0	ab
26	76.3	f-l	71.8	fgh	93.1	a	74.7	e-i	66.1	d-g	90.0	ab
27	82.3	b-k	83.3	a-f	91.3	a	77.0	b-i	75.6	a-f	92.1	ab
28	71.0	lk	62.6	h	89.6	a	67.0	i	59.8	g	84.3	ab
SEQ 1001	75.6	g-l	73.8	e-g	93.6	a	71.8	ghi	68.3	b-g	92.6	a
SEQ 1004	82.5	b-k	76.7	b-g	92.7	a	76.7	c-i	76.5	a-e	92.2	ab
SEQ 1008	82.3	b-k	72.9	fgh	94.3	a	79.5	a-h	70.5	c-g	91.4	ab
SEQ 1012	71.7	jkl	73.6	e-g	93.1	a	66.6	i	69.7	c-g	90.5	ab
SEQ 1014	76.9	e-l	72.2	fgh	92.2	a	72.9	f-i	69.0	c-g	90.6	ab
34	84.7	a-i	74.5	d-g	94.2	a	77.5	b-i	72.7	a-f	93.8	a
Ulonzo	90.5	a-d	86.2	a-d	93.2	a	86.9	a-d	79.8	ab	91.6	ab
WH	88.0	a-f	80.6	a-g	92.4	a	80.0	a-h	66.7	c-g	90.7	ab
Mean	82.8		77.9		92.3		78.0		72.7		89.6	
SE	2.7		2.8		3.6		2.5		2.9		3.4	
CV (%)	8.4		6.4		11.2		7.3		8.4		4.6	

Means followed by the same letter in columns are not significantly different at 0.05 Probability level (DMRT).

[1], PS, predawn stressed; MS, midday water stressed; MNS, midday non-stressed treatments

Table 12 (continued)

Genotype	29 DAE PS		MS		MNS		36 DAE PS		MS		MNS	
1	81.4	a-f	71.1	a-e	82.1	ab	79.9	abc	64.5	a-k	76.2	c-f
2	84.0	a-d	77.2	a	87.6	ab	78.1	a-d	73.8	abc	84.0	a-e
3	80.7	a-f	76.3	ab	86.1	ab	78.7	a-d	70.7	a-e	82.0	a-e
4	88.8	a	77.9	a	82.7	ab	83.2	a	76.1	a	79.3	a-f
5	75.9	b-k	63.2	c-j	89.4	a	72.6	a-h	57.6	g-k	80.3	a-e
6	77.3	a-xi	63.5	c-j	89.3	a	60.8	hij	56.5	i-k	91.3	a
7	83.4	a-e	75.1	abc	83.2	ab	63.1	f-j	73.1	a-d	83.1	a-e
8	80.2	a-g	72.5	a-d	85.7	ab	78.8	a-d	70.2	a-f	77.4	b-f
9	71.7	e-l	74.6	abc	85.5	ab	71.2	a-i	73.5	abc	83.6	a-e
10	63.9	klm	54.6	j	76.9	b	58.4	j	50.1	l	67.7	f
11	79.6	a-h	76.7	ab	86.7	ab	67.9	c-j	72.4	a-d	82.4	a-e
KatB9	76.5	b-j	75.2	abc	89.6	a	68.3	c-j	69.8	a-f	88.4	abc
GLPx92	85.4	ab	77.1	ab	89.1	a	83.1	a	75.7	ab	85.3	a-e
GLP1004	71.5	e-l	61.0	d-j	81.2	ab	66.7	d-j	59.8	e-k	77.6	b-f
Okuodo	80.0	a-h	74.6	abc	87.2	ab	63.5	f-j	63.8	b-k	84.6	a-e
16	72.1	d-l	71.7	a-e	88.2	ab	63.5	f-j	68.5	a-i	80.5	a-e
Kat B1	73.2	c-l	73.1	abc	80.1	ab	64.4	f-j	68.7	a-h	78.2	b-f
GLP 2	65.0	j-m	59.9	e-j	89.3	a	61.6	g-j	58.2	f-k	78.2	b-f
19	79.1	a-h	74.2	abc	82.1	ab	74.6	a-f	73.1	a-d	79.4	a-f
20	68.2	g-m	57.7	g-j	88.2	ab	63.8	f-j	54.8	jkl	82.3	a-e
21	68.0	h-m	71.7	a-e	89.2	a	66.7	d-j	63.7	b-k	84.9	a-e
22	79.3	a-h	67.8	a-i	89.7	a	72.9	a-h	66.8	a-j	89.0	ab
23	65.5	i-m	58.2	g-j	89.8	a	62.4	g-j	56.6	i-k	88.4	abc
24	71.7	e-l	68.5	a-h	87.8	ab	70.6	b-i	68.4	a-i	87.5	abc
Mbalaria	74.6	b-l	70.8	a-f	88.5	ab	73.6	a-g	63.2	c-k	74.2	ef
26	59.0	m	58.9	f-j	90.8	a	58.4	j	54.5	kl	89.6	ab
27	71.1	f-l	74.4	abc	89.9	a	67.6	d-j	73.8	abc	88.6	ab
28	63.7	lm	56.4	ij	82.4	ab	60.0	ij	54.1	kl	75.0	def
SEQ 1001	70.4	f-m	67.1	a-i	91.2	a	64.8	e-j	61.2	d-k	88.3	abc
SEQ 1004	73.9	b-l	71.7	a-e	88.6	ab	68.0	c-j	71.0	a-e	83.2	a-e
SEQ 1008	78.9	a-h	69.6	a-g	90.5	a	76.8	a-e	67.2	a-i	87.7	abc
SEQ 1012	66.1	i-m	57.2	hij	88.3	ab	65.4	e-j	56.8	h-k	89.6	ab
SEQ 1014	71.7	e-l	63.2	c-j	89.6	a	70.8	b-i	59.3	e-k	86.7	a-d
34	75.9	b-k	70.8	a-f	88.0	ab	74.6	a-f	69.5	a-g	89.5	ab
Ulonzo	85.1	abc	75.1	abc	90.0	a	81.6	ab	74.4	abc	89.2	ab
WH	76.7	b-j	65.0	b-j	90.6	a	71.4	a-i	64.5	a-k	87.9	abc
Mean	74.7		68.7		87.1		69.7		65.4		83.4	
SE	2,1		2.5		3.6.7		2.7		2.2		3.4	
CV (%)	11.0		8.8		13.5		8.7		10.3		11.8	

Means followed by the same letter in columns are not significantly different at 0.05 Probability level (DMRT).

¶, PS, predawn stressed; MS, midday water stressed; MNS, midday non-stressed treatments

Table 13. Predawn and midday leaf relative water content (RWC) for 36 dry bean genotypes measured at sampling episodes under field water stress and non-stress conditions during May – July (season 2) at Kiboko.

	15 DAE						22 DAE					
Genotype	PS[1]		MS		MNS		PS		MS		MNS	
1	88.4	a-e	79.6	d-h	94.1	a	81.8	d-i	77.7	c-j	92.7	a
2	92.9	abc	90.2	a	91.7	a	89	abc	87.5	ab	90.9	a
3	87.4	b-f	83.4	a-g	90.9	a	84.7	a-f	80.4	c-h	89.9	a
4	94.8	a	88.6	ab	91.5	a	90.4	a	88.0	a	90.7	a
5	84.4	efg	81.8	b-g	95.6	a	82	c-i	78.1	c-j	92.4	a
6	89.7	a-e	82.1	a-g	90.5	a	76.1	h-m	74.0	g-l	89.8	a
7	80.4	fgh	78.9	e-h	92.7	a	76.6	g-m	78.0	c-j	91.7	a
8	93.7	ab	88.0	abc	93.4	a	85.9	a-f	82.1	a-e	93.1	a
9	88.2	a-e	84.4	a-g	89.6	a	80.3	d-k	74.7	f-l	89.3	a
10	62.5	k	61.3	k	91.2	a	62.2	p	60.8	o	88.1	a
11	91.9	a-d	84.7	a-g	91.8	a	85.6	a-f	73.1	i-l	89.6	a
KatB9	86.1	c-g	86.7	a-e	92.6	a	85.4	a-f	82.8	a-d	91.5	a
GLPx92	92.2	a-d	79.1	e-h	93.6	a	86.7	a-d	84.5	abc	90.4	a
GLP1004	85.1	d-g	65.9	ijk	94.4	a	79.1	f-l	73.6	h-l	93.7	a
Okuodo	67.8	jk	82.1	a-g	90.4	a	66.4	op	64.6	mno	89.5	a
16	85.9	c-g	85.6	a-f	90.1	a	83.8	a-g	72.4	i-l	89.8	a
Kat B1	87.5	b-f	72.6	hij	93.2	a	79.4	e-l	81.7	a-f	92.4	a
GLP 2	86.1	c-g	84.9	a-g	94.2	a	75.3	i-m	70.4	klm	93.2	a
19	87.5	b-f	73.3	hi	95.0	a	79.7	d-l	76.6	d-k	93.5	a
20	75.9	hi	78.1	fgh	89.9	a	67.4	nop	72.0	i-l	88.7	a
21	80	gh	84.1	a-g	92.6	a	71	mno	76.8	d-k	90.4	a
22	86	c-g	77.5	fgh	94.5	a	83.4	a-g	78.1	c-j	93.9	a
23	83.7	efg	84.5	a-g	91.5	a	75.6	i-m	77.3	c-k	90.2	a
24	88.4	a-e	81.9	a-g	93.2	a	73.5	k-n	71.0	j-l	91.5	a
Mbalaria	85	d-g	82.0	a-g	92.3	a	80.7	d-j	75.2	e-k	90.6	a
26	90.1	a-e	77.8	fgh	90.5	a	79.7	d-l	63.3	no	87.6	a
27	85.1	d-g	85.1	a-g	94.7	a	83.3	a-g	80.4	c-h	89.3	a
28	69.6	ij	61.3	k	92.2	a	65	op	60.7	o	87.7	a
SEQ 1001	85.1	d-g	82.1	a-g	92.6	a	83.2	b-h	78.5	c-i	91.4	a
SEQ 1004	87.8	a-e	85.2	a-g	90.8	a	79.9	d-l	80.9	b-g	88.6	a
SEQ 1008	84.5	efg	76.9	gh	91.2	a	73.6	j-n	72.7	i-l	90.4	a
SEQ 1012	77.1	h	73.3	hi	93.9	a	77	g-m	67.9	lmn	91.8	a
SEQ 1014	73.9	hij	65.5	jk	92.6	a	65.2	op	64.5	mno	91.4	a
34	87.2	b-f	79.7	c-h	91.4	a	73	lmn	67.8	lmn	90.7	a
Ulonzo	92.7	abc	87.5	a-d	93.3	a	89.9	ab	81.2	a-g	92.4	a
WH	91.9	a-d	82.0	a-g	93.5	a	86.4	a-e	78.3	c-i	91.4	a
Mean	84.9		79.9		92.4		78.8		75.2		90.8	
SE	1.9		2.3		3.4		2.4		2.3		2.9	
CV (%)	9.5		7.9		10.2		6.5		6.2		9.6	

Means followed by the same letter in columns are not significantly different at 0.05 Probability level (DMRT).

[1], PS, predawn stressed; MS, midday water stressed; MNS, midday non-stressed treatments

Table 13 (continued)

Genotype	29 DAE PS[1]		MS		MNS		36 DAE PS		MS		MNS	
1	76.1	d-i	73.2	e-i	89.3	ab	75.2	b-h	66.5	e-i	87.4	abc
2	83.3	a-d	82.9	ab	88.0	ab	82.7	a	81.1	a	89.1	abc
3	76.2	d-i	74.6	c-h	87.5	ab	70.1	f-i	66.7	d-i	85.6	abc
4	88.5	a	84.2	a	89.3	ab	82.1	ab	81.5	a	88.1	abc
5	75.3	f-i	75.0	c-h	90.0	ab	72.5	fgh	65.7	f-i	89.5	abc
6	74.6	f-i	73.0	e-i	86.3	ab	70.0	ghi	64.4	ghi	84.2	bc
7	67.7	j-m	68.6	h-k	92.0	a	64.4	ijk	60.6	ij	89.6	abc
8	80.1	b-f	80.4	a-d	90.4	ab	79.8	a-e	65.0	ghi	87.8	abc
9	75.5	e-i	70.2	f-j	88.1	ab	71.2	f-i	64.5	ghi	84.4	abc
10	58.1	n	54.0	o	85.4	ab	57.5	lm	52.0	k	84.4	abc
11	82.6	a-e	67.9	h-k	88.3	ab	81.0	a-d	67.4	c-i	86.4	abc
KatB9	83.9	abc	80.8	abc	87.6	ab	82.6	a	73.3	b-e	86.8	abc
GLPx92	77.6	b-h	77.4	a-f	90.1	ab	76.3	a-g	74.3	bc	88.7	abc
GLP1004	76.2	d-i	71.4	e-j	92.2	a	74.0	d-h	62.0	i	90.4	abc
Okuodo	61.6	mn	60.3	l-o	85.5	ab	60.2	klm	51.5	k	87.8	abc
16	81.2	b-f	71.6	e-j	86.3	ab	72.8	e-h	70.7	b-g	83.5	c
Kat B1	74.8	f-i	78.4	a-e	90.3	ab	72.3	fgh	71.3	b-g	89.3	abc
GLP 2	72.2	g-j	69.3	g-k	90.1	ab	68.6	hij	61.5	ij	91.6	a
19	78.7	b-g	76.3	b-g	91.7	a	74.9	c-h	65.6	f-i	90.1	abc
20	63.3	lmn	56.2	no	87.4	ab	62.4	jkl	53.5	k	84.2	bc
21	70.6	h-k	73.4	d-i	91.5	ab	69.0	hij	72.3	b-f	90.6	abc
22	83.1	a-d	76.0	b-g	92.1	a	70.3	f-i	73.7	bcd	90.9	ab
23	75.6	e-i	68.5	h-k	88.4	ab	75.5	b-h	65.9	f-i	85.7	abc
24	69.6	i-l	65.0	j-m	90.7	ab	64.9	ijk	53.2	k	87.3	abc
Mbalaria	78.6	b-g	74.7	c-h	89.7	ab	70.3	f-i	70.5	b-g	87.5	abc
26	76.3	d-i	60.0	mno	84.3	b	75.8	a-h	53.7	k	84.6	abc
27	82.6	a-e	75.1	c-h	87.5	ab	69.7	ghi	64.7	ghi	85.9	abc
28	60.8	n	58.7	mno	85.2	ab	55.3	m	51.2	k	84.4	abc
SEQ 1001	80.6	b-f	72.8	e-i	90.1	ab	74.8	c-h	69.3	c-h	90.0	abc
SEQ 1004	76.8	c-i	72.3	e-i	86.3	ab	64.7	ijk	63.2	hi	85.8	abc
SEQ 1008	72.6	g-j	70.0	g-j	88.1	ab	70.7	f-i	67.4	c-i	87.5	abc
SEQ 1012	64.3	k-n	62.7	k-n	89.4	ab	61.2	klm	55.4	jk	87.8	abc
SEQ 1014	64.8	k-n	60.9	lmn	90.3	ab	62.4	jkl	53.8	k	89.8	abc
34	72.5	g-j	66.8	i-l	90.3	ab	64.3	ijk	64.2	ghi	89.2	abc
Ulonzo	84.5	ab	78.5	a-e	90.3	ab	81.4	abc	76.4	ab	89.9	abc
WH	81.1	b-f	76.4	b-g	91.5	ab	77.3	a-f	70.5	b-g	90.3	abc
Mean	75.1		71.0		88.9		71.1		65.1		87.7	
SE	2.4		2.32		2.3		2.5		2.4		3.2	
CV (%)	6.7		8.9		7.2		7.1		9.1		6.3	

Means followed by the same letter in columns are not significantly different at 0.05 Probability level (DMRT).

[1], PS, predawn stressed; MS, midday water stressed; MNS, midday non-stressed treatments

4.1.2 Leaf Water Potential (LWP)

The genotype x irrigation interaction effect was significant ($P<0.01$) at all sampling episodes in both seasons except at 15 DAE (Tables 14 and 15). Predawn LWP values were generally higher than the midday LWP values in both seasons at all sampling episodes (Tables 16 and 17). In both seasons, leaf water stress as measured by the LWP increased as the season progressed from 15 DAE to 36 DAE.

Siginificant genotypic differences were also detected at all sampling episodes in both seasons mainly in the WS than in the NS treatment. For example, under WS treatment during the first season, the predawn LWP values ranged from -0.25 MPa to -0.05 MPa, -0.36 MPa to -0.12 MPa, -0.72 MPa to -0.36 MPa and from -0.14 MPa to -0.36 MPa in 15, 22, 29, and 36 DAE, respectively. The genotypes that had relatively higher values were 2 (Ex-Kitui), 4 (Ex-Embu), Ulonzo, and GLP x 92, 8 (Ex-Kirinyaga), KAT B1 and KAT B9. In contrast, genotypes, 10 (Ex-Nyeri), 20 (Ex-Nyeri), 22 (Ex-Taita) and 23 (Ex-Meru) consistently showed lower LWP values at all sampling episodes. These trends were also observed on the midday LWP values, for example, during the first season, the LWP values ranged from –0.25 MPa to -0.10 MPa, -0.36 MPa to –0.14 MPa, -0.76 MPa to –0.38 MPa and –1.17 MPa to –0.65 MPa at 15, 22, 29, and 36 DAE, respectively.

Table 14. Predawn LWP mean squares from analysis of variance at 15, 22, 29 and 36 DAE for January-March 1996 (season 1) and May-July 1996 (season 2) at Kiboko.

Source of variation	df	Mean Squares							
		Season 1				Season 2			
		15 DAE	22 DAE	29 DAE	36 DAE	15 DAE	22 DAE	29 DAE	36 DAE
Irrigation	1	0.12	0.22	0.21	0.18	0.28	0.25	0.15	0.20
Rep (Irrig)	2	0.02	0.01	0.00	0.01	0.00	0.02	0.00	0.00
Error (a)	2	0.19	0.33	0.47	0.36	0.43	0.35	0.29	0.31
Genotypes	35	0.91	0.24*	0.43**	0.61**	0.55	0.29*	0.34**	0.21**
Genotype x irrigation	35	0.11	0.14	0.38*	0.54**	0.20	0.18*	0.13**	0.30**
Error (b)	70	0.89	0.25	0.26	0.19	0.49	0.11	0.03	0.09

***, ** significant at P< 0.05 and 0.01 levels, respectively.**

Table 15. Midday LWP mean squares from analysis of variance at 15, 22, 29 and 36 DAE for January - March 1996 (season 1) and May - July 1996 (season 2) at Kiboko.

Source of variation	df	Mean Squares							
		Season 1				Season 2			
		15 DAE	22 DAE	29 DAE	36 DAE	15 DAE	22 DAE	29 DAE	36 DAE
Irrigation	1	0.23	0.25	0.01	0.02	0.28	0.25	0.15	0.20
Rep (Irrig)	2	0.02	0.01	0.00	0.01	0.00	0.02	0.00	0.00
Error (a)	2	0.52	0.47	0.03	0.04	0.54	0.34	0.26	0.33
Genotypes	35	0.91*	0.24**	0.43**	0.41**	0.55*	0.29**	0.34**	0.21**
Genotype x irrigation	35	0.11	0.14*	0.38**	0.54**	0.20	0.18**	0.13**	0.30**
Error (b)	70	0.29	0.09	0.22	0.09	0.19	0.11	0.03	0.09

***, ** significant at P< 0.05 and 0.01 levels, respectively.**

Table 16. **Predawn and midday means for leaf water potential (LWP) for 36 dry bean genotypes measured at four sampling episodes under field water stress and non-stress conditions during January - March 1996 (season 1) at Kiboko .**

	15 DAE						22 DAE					
Genotype	PS[1]		MS		MNS		PS		MS		MNS	
1	-0.19	bcd	-0.11	a	-0.05	a	-0.30	efg	-0.34	d-i	-0.11	a
2	-0.05	a	-0.10	a	-0.01	a	-0.18	abc	-0.20	abc	-0.08	a
3	-0.13	a-d	-0.16	a-e	-0.04	a	-0.24	b-f	-0.24	a-d	-0.11	a
4	-0.10	ab	-0.10	a	-0.05	a	-0.12	a	-0.17	ab	-0.09	a
5	-0.20	bcd	-0.20	a-e	-0.09	a	-0.30	efg	-0.36	f-i	-0.11	a
6	-0.15	a-d	-0.20	a-e	-0.02	a	-0.28	c-g	-0.28	c-g	-0.08	a
7	-0.15	a-d	-0.15	a-e	-0.08	a	-0.20	a-e	-0.22	abc	-0.10	a
8	-0.10	ab	-0.15	a-e	-0.08	a	-0.24	b-f	-0.23	abc	-0.09	a
9	-0.11	abc	-0.15	a-e	-0.10	a	-0.18	abc	-0.24	a-d	-0.11	a
10	-0.21	cd	-0.18	a-e	-0.10	a	-0.30	efg	-0.37	g-j	-0.11	a
11	-0.11	abc	-0.24	de	-0.10	a	-0.24	b-f	-0.35	e-i	-0.10	a
KatB9	-0.10	ab	-0.11	a	-0.05	a	-0.19	a-d	-0.24	a-d	-0.10	a
GLPx92	-0.10	ab	-0.10	a	-0.10	a	-0.14	ab	-0.22	abc	-0.10	a
GLP1004	-0.15	a-d	-0.12	ab	-0.10	a	-0.25	c-f	-0.30	c-h	-0.10	a
Okuodo	-0.16	bcd	-0.14	a-d	-0.10	a	-0.36	g	-0.34	d-i	-0.11	a
16	-0.11	abc	-0.15	a-e	-0.10	a	-0.28	c-g	-0.34	d-i	-0.11	a
Kat B1	-0.10	ab	-0.12	ab	-0.08	a	-0.18	abc	-0.22	abc	-0.10	a
GLP 2	-0.12	abc	-0.12	ab	-0.10	a	-0.28	c-g	-0.30	c-h	-0.11	a
19	-0.10	ab	-0.23	cde	-0.05	a	-0.36	g	-0.28	c-g	-0.11	a
20	-0.20	bcd	-0.25	e	-0.05	a	-0.32	fg	-0.46	j	-0.05	a
21	-0.20	bcd	-0.25	e	-0.08	a	-0.29	d-g	-0.40	hij	-0.10	a
22	-0.23	d	-0.25	e	-0.10	a	-0.31	fg	-0.42	ij	-0.10	a
23	-0.20	bcd	-0.20	a-e	-0.05	a	-0.25	c-f	-0.26	b-f	-0.10	a
24	-0.15	a-d	-0.18	a-e	-0.08	a	-0.24	b-f	-0.26	b-f	-0.10	a
Mbalaria	-0.13	a-d	-0.13	abc	-0.10	a	-0.22	a-f	-0.30	c-h	-0.10	a
26	-0.11	abc	-0.18	a-e	-0.10	a	-0.22	a-f	-0.29	c-g	-0.12	a
27	-0.12	abc	-0.16	a-e	-0.04	a	-0.28	c-g	-0.30	c-h	-0.11	a
28	-0.17	bcd	-0.20	a-e	-0.08	a	-0.24	b-f	-0.36	f-i	-0.10	a
SEQ 1001	-0.16	bcd	-0.20	a-e	-0.10	a	-0.25	c-f	-0.29	c-g	-0.10	a
SEQ 1004	-0.14	a-d	-0.18	a-e	-0.08	a	-0.24	b-f	-0.26	b-f	-0.11	a
SEQ 1008	-0.15	a-d	-0.20	a-e	-0.10	a	-0.28	c-g	-0.29	c-g	-0.11	a
SEQ 1012	-0.18	bcd	-0.20	a-e	-0.09	a	-0.31	fg	-0.36	f-i	-0.11	a
SEQ 1014	-0.18	bcd	-0.22	b-e	-0.11	a	-0.28	c-g	-0.34	d-i	-0.11	a
34	-0.19	bcd	-0.20	a-e	-0.11	a	-0.29	d-g	-0.37	g-j	-0.10	a
Ulonzo	-0.10	ab	-0.11	a	-0.05	a	-0.24	b-f	-0.14	a	-0.10	a
WH	-0.12	abc	-0.15	a-e	-0.10	a	-0.22	a-f	-0.25	b-e	-0.11	a
Mean	-0.14		-0.17		-0.08		-0.25		-0.29		-0.10	
SE	0.006		0.008		0.009		0.007		0.005		0.007	
CV (%)	18.0		21.1		13.5		19.5		12.1		9.1	

Means followed by the same letter in columns are not significantly different at 0.05 Probability level (DMRT).

[1], PS, predawn stressed; MS, midday water stressed; MNS, midday non-stressed treatments

Table 16. (continued)

Genotype	29 DAE						36 DAE					
	PS[¶]		MS		MNS		PS		MS		MNS	
1	-0.57	e-i	-0.57	d-h	-0.13	a	-0.99	ef	-1.17	j	-0.12	a
2	-0.36	a	-0.38	a	-0.08	a	-0.60	a	-0.65	a	-0.10	a
3	-0.44	abc	-0.57	d-h	-0.12	a	-0.78	bc	-0.99	ghi	-0.11	a
4	-0.40	ab	-0.42	ab	-0.12	a	-0.73	b	-0.78	bc	-0.11	a
5	-0.57	e-i	-0.57	d-h	-0.12	a	-1.04	f	-1.17	j	-0.12	a
6	-0.46	a-d	-0.53	c-g	-0.11	a	-0.73	b	-0.99	ghi	-0.10	a
7	-0.48	b-e	-0.53	c-g	-0.12	a	-0.86	cd	-1.04	hi	-0.12	a
8	-0.48	b-e	-0.49	b-e	-0.11	a	-0.73	b	-0.78	bc	-0.11	a
9	-0.57	e-i	-0.51	b-f	-0.11	a	-0.91	de	-0.70	ab	-0.10	a
10	-0.57	e-i	-0.67	hij	-0.11	a	-0.99	ef	-1.17	j	-0.10	a
11	-0.44	abc	-0.57	d-h	-0.11	a	-0.86	cd	-0.78	bc	-0.12	a
KatB9	-0.42	ab	-0.46	abc	-0.11	a	-0.78	bc	-0.78	bc	-0.10	a
GLPx92	-0.48	b-e	-0.51	b-f	-0.11	a	-0.86	cd	-0.81	cd	-0.11	a
GLP1004	-0.48	b-e	-0.53	c-g	-0.10	a	-0.78	bc	-0.99	ghi	-0.11	a
Okuodo	-0.55	d-h	-0.59	e-h	-0.11	a	-0.99	ef	-0.99	ghi	-0.11	a
16	-0.63	g-j	-0.57	d-h	-0.10	a	-0.99	ef	-1.04	hi	-0.11	a
Kat B1	-0.46	a-d	-0.53	c-g	-0.11	a	-0.94	def	-0.88	def	-0.10	a
GLP 2	-0.63	g-j	-0.57	d-h	-0.11	a	-0.99	ef	-1.07	ij	-0.12	a
19	-0.72	j	-0.67	hij	-0.11	a	-1.04	f	-0.99	ghi	-0.12	a
20	-0.67	ij	-0.76	j	-0.10	a	-1.14	g	-1.17	j	-0.10	a
21	-0.67	ij	-0.67	hij	-0.11	a	-0.94	def	-1.04	hi	-0.11	a
22	-0.67	ij	-0.72	ij	-0.11	a	-1.01	ef	-1.17	j	-0.11	a
23	-0.57	e-i	-0.63	ghi	-0.11	a	-0.86	cd	-0.99	ghi	-0.10	a
24	-0.46	a-d	-0.53	c-g	-0.11	a	-0.88	cd	-0.91	efg	-0.11	a
Mbalaria	-0.44	abc	-0.53	c-g	-0.11	a	-0.91	de	-1.04	hi	-0.10	a
26	-0.53	c-g	-0.48	bcd	-0.11	a	-0.88	cd	-1.07	ij	-0.10	a
27	-0.48	b-e	-0.72	ij	-0.12	a	-0.94	def	-1.04	hi	-0.10	a
28	-0.53	c-g	-0.67	hij	-0.10	a	-0.91	de	-1.17	j	-0.11	a
SEQ 1001	-0.53	c-g	-0.48	bcd	-0.12	a	-0.78	bc	-0.83	cde	-0.11	a
SEQ 1004	-0.49	b-f	-0.57	d-h	-0.12	a	-0.78	bc	-1.17	j	-0.10	a
SEQ 1008	-0.65	hij	-0.61	fgh	-0.10	a	-1.01	ef	-1.07	ij	-0.10	a
SEQ 1012	-0.57	e-i	-0.61	fgh	-0.12	a	-1.04	f	-1.09	ij	-0.10	a
SEQ 1014	-0.57	e-i	-0.65	hi	-0.12	a	-0.91	de	-0.94	fgh	-0.10	a
34	-0.57	e-i	-0.67	hij	-0.05	a	-0.94	def	-1.17	j	-0.10	a
Ulonzo	-0.44	abc	-0.46	abc	-0.05	a	-0.73	b	-0.86	c-f	-0.11	a
WH	-0.59	f-i	-0.63	ghi	-0.11	a	-0.94	def	-1.04	hi	-0.10	a
Mean	-0.53		-0.57		-0.11		-0.89		-0.99		-0.11	
SE	0.007		0.11		0.09		0.09		0.008		0.12	
CV (%)	17.5		19.2		12.3		13.4		15.9		23.1	

Means followed by the same letter in columns are not significantly different at 0.05 Probability level (DMRT).

[¶], PS, predawn stressed; MS, midday water stressed; MNS, midday non-stressed treatments

Table 17. **Predawn and midday means for leaf water potential (LWP) for 36 dry bean genotypes measured at four sampling episodes under field water stress and non-stress conditions during May – July, 1996 (season 2) at Kiboko.**

	15 DAE						22 DAE					
Genotype	PS[1]		MS		MNS		PS		MS		MNS	
1	-0.13	bc	-0.23	ef	-0.05	a	-0.22	bcd	-0.28	bc	-0.08	a
2	-0.05	a	-0.12	ab	-0.05	a	-0.13	a	-0.17	a	-0.10	ab
3	-0.15	bcd	-0.21	def	-0.10	a	-0.28	def	-0.29	bc	-0.10	ab
4	-0.10	ab	-0.10	a	-0.05	a	-0.16	ab	-0.14	a	-0.10	ab
5	-0.15	bcd	-0.23	ef	-0.10	a	-0.29	ef	-0.30	bcd	-0.10	ab
6	-0.18	cd	-0.24	ef	-0.08	a	-0.28	def	-0.29	bc	-0.10	ab
7	-0.18	cd	-0.18	b-e	-0.08	a	-0.24	cde	-0.30	bcd	-0.08	a
8	-0.10	ab	-0.12	ab	-0.08	a	-0.18	abc	-0.24	b	-0.13	ab
9	-0.20	d	-0.18	b-e	-0.10	a	-0.13	a	-0.34	cde	-0.15	b
10	-0.20	d	-0.18	b-e	-0.10	a	-0.26	def	-0.36	def	-0.10	ab
11	-0.15	bcd	-0.20	c-f	-0.08	a	-0.24	cde	-0.30	bcd	-0.10	ab
KatB9	-0.10	ab	-0.11	a	-0.10	a	-0.24	cde	-0.17	a	-0.10	ab
GLPx92	-0.11	ab	-0.10	a	-0.10	a	-0.18	abc	-0.24	b	-0.10	ab
GLP1004	-0.18	cd	-0.14	abc	-0.10	a	-0.26	def	-0.34	cde	-0.10	ab
Okuodo	-0.14	bcd	-0.20	c-f	-0.10	a	-0.28	def	-0.36	def	-0.11	ab
16	-0.18	cd	-0.14	abc	-0.10	a	-0.29	ef	-0.31	cd	-0.10	ab
Kat B1	-0.10	ab	-0.12	ab	-0.10	a	-0.17	ab	-0.24	b	-0.11	ab
GLP 2	-0.13	bc	-0.16	a-d	-0.10	a	-0.29	ef	-0.36	def	-0.12	ab
19	-0.12	bc	-0.13	ab	-0.10	a	-0.30	ef	-0.28	bc	-0.11	ab
20	-0.20	d	-0.25	f	-0.10	a	-0.30	ef	-0.41	f	-0.11	ab
21	-0.20	d	-0.18	b-e	-0.11	a	-0.26	def	-0.34	cde	-0.11	ab
22	-0.20	d	-0.25	f	-0.10	a	-0.29	ef	-0.42	f	-0.11	ab
23	-0.16	bcd	-0.20	c-f	-0.10	a	-0.24	cde	-0.40	ef	-0.10	ab
24	-0.11	ab	-0.23	ef	-0.08	a	-0.24	cde	-0.31	cd	-0.10	ab
Mbalaria	-0.11	ab	-0.20	c-f	-0.10	a	-0.22	bcd	-0.28	bc	-0.10	ab
26	-0.10	ab	-0.23	ef	-0.10	a	-0.24	cde	-0.28	bc	-0.11	ab
27	-0.11	ab	-0.15	a-d	-0.10	a	-0.24	cde	-0.28	bc	-0.10	ab
28	-0.14	bcd	-0.20	c-f	-0.10	a	-0.29	ef	-0.28	bc	-0.11	ab
SEQ 1001	-0.18	cd	-0.25	f	-0.10	a	-0.24	cde	-0.30	bcd	-0.10	ab
SEQ 1004	-0.10	ab	-0.20	c-f	-0.08	a	-0.16	ab	-0.30	bcd	-0.10	ab
SEQ 1008	-0.15	bcd	-0.18	b-e	-0.10	a	-0.29	ef	-0.31	cd	-0.11	ab
SEQ 1012	-0.20	d	-0.23	ef	-0.10	a	-0.28	def	-0.30	bcd	-0.11	ab
SEQ 1014	-0.12	bc	-0.23	ef	-0.10	a	-0.29	ef	-0.34	cde	-0.10	ab
34	-0.15	bcd	-0.20	c-f	-0.10	a	-0.31	f	-0.36	def	-0.11	ab
Ulonzo	-0.14	bcd	-0.11	a	-0.10	a	-0.19	abc	-0.17	a	-0.11	ab
WH	-0.18	cd	-0.20	c-f	-0.10	a	-0.24	cde	-0.30	bcd	-0.11	ab
Mean	-0.14		-0.18		0.09		-0.24		-0.30		-0.11	
SE	0.003		0.03		0.04		0.05		0.04		0.03	
CV (%)	20.0		19.2		12.9		18.4		17.5		16.8	

Means followed by the same letter in columns are not significantly different at 0.05 Probability level (DMRT).

[1], PS, predawn stressed; MS, midday water stressed; MNS, midday non-stressed treatments

Table 17 (continued)

Genotype	29 DAE						36 DAE					
	PS[¶]		MS		MNS		PS		MS		MNS	
1	-0.53	def	0.57	a	-0.08	a	-0.99	hi	-1.12	hij	-0.10	a
2	-0.34	a	-0.38	b	-0.11	ab	-0.68	b	-0.62	a	-0.12	a
3	-0.49	cde	-0.57	ef	-0.11	ab	-1.01	i	-0.99	d-h	-0.14	a
4	-0.38	ab	-0.42	bc	-0.11	ab	-0.62	a	-0.73	ab	-0.13	a
5	-0.55	ef	-0.63	fg	-0.11	ab	-0.99	hi	-0.94	d-g	-0.11	a
6	-0.46	cd	-0.53	de	-0.10	ab	-0.81	de	-0.88	cde	-0.11	a
7	-0.46	cd	-0.59	ef	-0.10	ab	-0.73	bc	-0.94	d-g	-0.14	a
8	-0.38	ab	-0.57	ef	-0.13	ab	-0.78	cd	-0.86	bcd	-0.12	a
9	-0.44	bc	-0.57	ef	-0.15	b	-0.88	fg	-1.07	ghi	-0.12	a
10	-0.44	bc	-0.67	g	-0.11	ab	-1.04	ij	-1.09	hi	-0.13	a
11	-0.42	bc	-0.53	de	-0.10	ab	-0.73	bc	-0.86	bcd	-0.10	a
KatB9	-0.44	bc	-0.46	c	-0.12	ab	-0.73	bc	-0.88	cde	-0.11	a
GLPx92	-0.44	bc	-0.53	de	-0.11	ab	-0.78	cd	-0.78	bc	-0.11	a
GLP1004	-0.63	gh	-0.63	fg	-0.13	ab	-0.83	def	-0.99	d-h	-0.12	a
Okuodo	-0.53	def	-0.67	g	-0.13	ab	-1.04	ij	-1.04	f-i	-0.12	a
16	-0.46	cd	-0.57	ef	-0.14	ab	-0.94	gh	-0.86	bcd	-0.12	a
Kat B1	-0.57	fg	-0.48	cd	-0.10	ab	-0.86	ef	-1.25	jk	-0.11	a
GLP 2	-0.57	fg	-0.63	fg	-0.11	ab	-0.94	gh	-0.94	d-g	-0.11	a
19	-0.68	h	-0.57	ef	-0.13	ab	-0.94	gh	-1.30	k	-0.13	a
20	-0.57	fg	-0.78	h	-0.11	ab	-1.04	ij	-1.01	e-h	-0.13	a
21	-0.54	ef	-0.63	fg	-0.13	ab	-0.88	fg	-1.04	f-i	-0.13	a
22	-0.58	fg	-0.67	g	-0.11	ab	-0.83	def	-1.07	ghi	-0.13	a
23	-0.48	cde	-0.67	g	-0.11	ab	-0.86	ef	-0.91	c-f	-0.13	a
24	-0.48	cde	-0.57	ef	-0.10	ab	-0.78	cd	-1.04	f-i	-0.11	a
Mbalaria	-0.44	bc	-0.61	fg	-0.12	ab	-0.83	def	-0.88	cde	-0.13	a
26	-0.48	cde	-0.63	fg	-0.13	ab	-0.78	cd	-1.07	ghi	-0.12	a
27	-0.49	cde	-0.67	g	-0.10	ab	-0.88	fg	-1.13	hij	-0.11	a
28	-0.57	fg	-0.67	g	-0.13	ab	-1.09	j	-1.17	ij	-0.13	a
SEQ 1001	-0.53	def	-0.59	ef	-0.12	ab	-0.83	def	-0.99	d-h	-0.11	a
SEQ 1004	-0.48	cde	-0.48	cd	-0.11	ab	-0.78	cd	-0.94	d-g	-0.12	a
SEQ 1008	-0.48	cde	-0.63	fg	-0.14	ab	-0.88	fg	-0.99	d-h	-0.11	a
SEQ 1012	-0.48	cde	-0.63	fg	-0.12	ab	-0.86	ef	-0.99	d-h	-0.12	a
SEQ 1014	-0.49	cde	-0.59	ef	-0.13	ab	-0.83	def	-0.91	c-f	-0.12	a
34	-0.53	def	-0.78	h	-0.12	ab	-1.04	ij	-1.17	ij	-0.11	a
Ulonzo	-0.44	bc	-0.48	cd	-0.12	ab	-0.73	bc	-0.78	bc	-0.11	a
WH	-0.44	bc	-0.53	de	-0.11	ab	-0.99	hi	-0.99	d-h	-0.10	a
Mean	-0.49		-0.56		-0.17		-0.87		-0.98		-0.12	
SE	0.08		0.12		0.09		0.13		0.12		0.09	
CV (%)	19.4		20.6		13.5		22.1		19.6		9.5	

Means followed by the same letter in columns are not significantly different at 0.05 Probability level (DMRT).

[¶], PS, predawn stressed; MS, midday water stressed; MNS, midday non-stressed treatments

4.1.3 Relative Growth Rate (RGR)

The genotype x irrigation interaction effects were significant ($P<0.01$) at both harvesting occassions (RGR1 and RGR 2) in both seasons. The genotype effect was also significant ($P<0.01$) at both RGR1 and RGR2 (Appendix 2). The RGR values were generally lower under WS compared to the NS treatment at all harvest occassions. For example, RGR values under WS treatment varied from 0.015 to 0.239g g^{-1} day^{-1} and from 0.031 to 0.241g g^{-1} day^{-1} at RGR1 and RGR2, respectively. Under the NS treatment, these values ranged from 0.023 to 0.411g g^{-1} day^{-1} and between 0.030 to 0.354g g^{-1} day^{-1} at RGR1 and RGR2, respectively (Table 18).

Under WS treatment, genotypes Ulonzo, GLP x 92 White Haricot, 4 (Ex-Embu), 5 (Ex-Kakamega), 16 (ex-Kitui), 6 (ex-Kakamega), and Kat B9 exhibited significantly higher ($P<0.05$) RGR1 and RGR2 values, while the genotypes which presented relatively lower RGR values were GLP2, 10 (Ex-Nyeri), 19 (Ex-Kakamega) Okuodo and 20 (Ex-Nyeri). Apparently, under the WS treatment, the same genotypes exhibited similar trends for the RWC and LWP values.

Under the NS treatment, higher RGR values were generally observed in genotypes that were collected from the higher rainfall areas than in the collections from the semi-arid areas. For example, genotypes 34 (Ex-Kiambu), 26 (Ex-Migori), 22 (Ex-Taita) and 11(Ex-Kisii) presented significantly higher ($P<0.05$) values, while GLP 1004, KAT B1 and GLP x 92 had relatively lower RGR values during both harvest occassions.

Table 18. **Means for Relative Growth Rates for 36 dry bean genotypes averaged over two seasons measured between seedling and pre-flowering (RGR1) and between pre-flowering and flowering growth stages (RGR2) under water stress (WS) and non-stress (NS) treatments at Kiboko.**

	RGR1		RGR2	
Genotype	WS	NS	WS	NS
1	0.029 h-k	0.099 e-k	0.089 def	0.030 j
2	0.066 d-k	0.085 f-k	0.105 def	0.083 f-j
3	0.075 c-k	0.089 f-k	0.083 def	0.117 d-j
4	0.135 b-f	0.148 b-z	0.214 ab	0.103 d-j
5	0.237 a	0.044 jk	0.112 c-f	0.133 d-j
6	0.159 bc	0.044 jk	0.024 f	0.063 hij
7	0.149 bcd	0.153 b-z	0.112 c-f	0.112 d-j
8	0.050 f-k	0.143 c-j	0.131 b-e	0.083 f-j
9	0.115 c-h	0.105 e-k	0.031 f	0.048 j
10	0.025 ijk	0.166 b-g	0.061 def	0.071 g-j
11	0.047 g-k	0.241 bc	0.234 a	0.224 bcd
KAT B9	0.149 bcd	0.164 b-h	0.085 def	0.195 b-g
GLP x 92	0.150 bcd	0.059 ijk	0.241 a	0.148 d-j
GLP 1004	0.015 k	0.023 k	0.062 def	0.079 f-j
Okuodo	0.106 c-j	0.103 e-k	0.139 bcd	0.096 e-f
16	0.213 ab	0.128 d-j	0.118 c-f	0.218 b-e
KAT B1	0.123 c-g	0.026 k	0.074 def	0.116 d-j
GLP 2	0.026 ijk	0.092 f-k	0.034 f	0.115 d-j
19	0.144 b-e	0.112 e-k	0.031 f	0.065 hij
20	0.002 ijk	0.081 g-k	0.037 ef	0.064 hij
21	0.072 c-k	0.064 h-k	0.058 def	0.092 e-j
22	0.144 b-e	0.159 b-z	0.035 ef	0.276abc
23	0.065 d-k	0.098 e-k	0.062 def	0.129 d-j
24	0.109 c-z	0.182 b-f	0.097 def	0.102 d-j
Mbalaria	0.058 e-k	0.195 b-e	0.101 def	0.099 d-j
26	0.079 c-k	0.128 d-j	0.136 bcd	0.295 ab
27	0.063 d-k	0.18 b-g	0.083 def	0.107 d-j
28	0.025 ijk	0.114 e-k	0.116 c-f	0.090 e-j
SEQ 1001	0.020 jk	0.142 d-j	0.075 def	0.117 d-j
SEQ 1004	0.136 b-f	0.195 b-e	0.076 def	0.171 c-z
SEQ 1008	0.072 c-k	0.119 d-k	0.154 a-d	0.204 b-f
SEQ 1012	0.025 ijk	0.161 b-h	0.199 abc	0.189 b-h
SEQ 1014	0.148 bcd	0.214 bcd	0.073 def	0.140 d-j
34	0.087 c-k	0.411 a	0.081 def	0.128 d-j
Ulonzo	0.239 a	0.148 b-z	0.035 ef	0.089 f-j
White Haricot	0.072 c-k	0.244 b	0.218 ab	0.354 a
Mean	0.096	0.135	0.101	0.131
SE	0.004	0.005	0.005	0.006
CV (%)	53.2	42.7	54.5	56.4

Means followed by the same letter in columns are not significantly different at 0.05 Probability level (DMRT).

4.1.4 Days to 50% Flowering (DTF)

The genotype and genotype x irrigation interaction effects were significant ($P<0.01$), indicating differential response of the genotypes to the two watering regimes (Table 19). Flowering was generally delayed in the NS treatment compared to the WS treatment in both seasons. For example during the first season, days to 50% flowering varied from 29 - 40 days, and 30 - 46 days under the WS and NS treatments, respectively (Tables 20).

In both seasons under the WS treatment, genotypes Ulonzo, 4 (Ex-Embu), 9 (Ex-Kitui), 10 (Ex-Nyeri), 11 (Ex-Kisii), 21 (Ex-Kiambu), 24 (Ex-Machakos), 27 (Ex-Kwale), 28 (Ex-Kisii), KAT B1, GLP x 92 and GLP 1004 were early in flowering (below 31 days). In comparison, Okuodo, 19 (Ex-Kakamega), 34 (Ex-Kiambu), SEQ 1001, SEQ 1004, SEQ 1008, SEQ 1012 and SEQ 1014 flowered relatively later (above 36 days). Similar trends for days to flowering were also observed under the NS treatment in both seasons. These results generally show that majority of the genotypes that were collected from the water limited areas were generally earlier in flowering compared to those collected from the higher rainfall areas under both watering regimes. The genotypes obtained from CIAT were predominantly later in flowering under both watering regimes.

It is of interest to note that some genotypes which had low plant water status under water stress, for example genotypes 10 (Ex-Nyeri), 21 (Ex-Nyeri) and 28 (Ex-Kisii) were also ealier in flowering under both watering regimes. These genotypes were also collections from the higher rainfall areas

Table 19. **Days to 50% flower mean squares for 36 dry bean genotypes grown under water stress (WS) and nonstress (NS) treatments during January–April 1996 (season 1) and during May–July 1996 (season 2) at Kiboko.**

		Mean squares	
Source of variation	df	Season 1	Season 1
Irrigation	1	227.56	301.62
Replication (irrigation)	2	18.17	33.16
Error (a)	2	321.23	331.19
Genotype	35	73.47**	118.82**
Genotype x Irrigation	35	10.56**	96.97**
Error (b)	70	2.45	3.65

** significant at $P < 0.01$.

Table 20. **Days to 50% flower means for 36 dry bean genotypes grown under water stress (WS) and nonstress (NS) treatments during January–April 1996 (season 1) and May–July 1996 (season 2) at Kiboko**

	Days to 50% flower			
	SEASON 1		SEASON 2	
Genotype	WS	NS	WS	NS
1	33 h-m	35 fgh	34 c-h	34 g-l
2	33 g-l	34 hi	34 c-h	36 f-i
3	34 f-k	34 hi	36 h-h	39 def
4	31 k-o	31 kl	34 c-h	36 f-i
5	33 h-m	35 fgh	34 c-h	39 def
6	34 f-k	40 d	35 b-h	40 de
7	36 b-f	40 d	38 a-e	40 de
8	32 j-o	32 ijk	34 c-h	35 g-j
9	30 mno	32 jkl	33 d-h	33 h-m
10	30 mno	34 hi	32 e-h	32 j-m
11	32 i-n	36 efg	31 fgh	35 g-j
KAT B9	32 j-o	32 jkl	31 fgh	32 j-m
GLP x 92	31 k-o	30 l	30 h	31 m
GLP 1004	31 l-o	34 hi	31gh	33 h-m
Okuodo	39 ab	46 a	38 a-e	44 ab
16	32 i-n	35 fgh	35 a-h	35 g-k
KAT B1	30 mno	32 jkl	31 fgh	32 j-m
GLP 2	34 f-k	36 efg	34 c-h	36 fgh
19	36 b-f	36 ef	39 abc	36 f-i
20	32 j-o	35 fgh	37 a-f	36 fgh
21	31 k-o	35 fgh	34 c-h	35 g-k
22	32 j-o	34 hi	35 b-h	34 g-l
23	35 d-h	42 bc	36 a-h	44 abc
24	31 l-o	33 hij	35 a-h	36 f-h
Mbalaria	33 h-m	36 efg	34 c-h	35 g-j
26	33 h-m	35 fgh	35 b-h	35 g-k
27	29 o	32 jkl	34 c-h	32 klm
28	30 no	34 hi	32 e-h	35 g-k
SEQ 1001	36 b-f	41 cd	37 a-f	42 a-d
SEQ 1004	36 c-g	40 d	39 abc	41 cd
SEQ 1008	38 a-d	40 d	39 abc	40 d
SEQ 1012	40 a	40 d	41 a	41 bcd
SEQ 1014	37 a-e	44 b	40 ab	45 a
34	36 b-f	37 e	38 a-e	37 efg
Ulonzo	31 k-o	34 gh	31 f-h	34 g-l
WH	36 b-f	40 d	38 a-d	39 def
SE	0.14	0.9	0.29	0.16
Mean	33	36	35	36
CV (%)	13.6	8.5	9.4	3.8

Means followed by the same letter in columns are not significantly different at 0.05 Probability level (DMRT).

4.2 Experiment II: Effect of water stress on root growth of dry bean genotypes.

The genotype and genotype x irrigation interaction effects were significant ($P<0.05$) at the two monitoring occassions (15 DAE and 36 DAE) for taproot length (TRL) and root dry weight (RDW (Appendix 3). Genotypic differences in root growth as measured by TRL and RDW at the two monitoring occasions were observed in both watering regimes. However, higher genotypic differences were observed under the WS treatment compared to the NS treatment at both monitoring occassions.

Under the water stress treatment (WST) at seedling stage (15 DAE), taproot length generally grew rapidly but accumulated less root dry weight compared to the non-stress (NST) treatment (Tables 21 and 22). However, at pod development (36 DAE), both the TRL and RDW values were generally reduced under WST compared to the NST treatment. At both monitoring occassions under WST, relatively rapid taproot length and dry weight accumulation were recorded in genotypes 2 (Ex-Kitui), 8 (Ex-Kirinyaga), KAT B1, KAT B9, Ulonzo, and GLP x 92 while slow growth values were observed in genotypes Okuodo, 3 (Ex-Kisii), 22 (Ex-Taita), 28 (Ex-Kisii) and 34 (Ex-Kiambu). CIAT genotypes generally had higher root growth values compared to the local collections during the second monitoring occasion (36 DAE) under both watering regimes. The genotypes that had higher root growth values under water stress also maintained higher plant water status values (RWC and LWP).

Table 21. **Taproot length (cm) means for 36 drybean genotypes measured at two occassions (15 and 36 DAE) under water stress (WST) and non-stress (NST) treatments for two seasons.**

	Taproot length (cm)			
	15 DAE		29 DAE	
Genotype	WST	NST	WST	NST
1	56.0 bed	44.7 a-g	57.7 l-p	76.7 a-d
2	59.3 ab	50.7 ab	82.0 a	80.3 a-d
3	40.7 k-n	38.7 e-m	58.3 op	80.3 a-d
4	58.7 ab	37.3 g-n	72.8 j-o	79.0 a-d
5	51.7 c-g	40.7 d-l	65.3 c-i	68.3 a-d
6	44.7 h-c	46.3 a-e	49.3 j-p	62.0 d
7	44.7 h-c	42.7 b-k	55.7 f-n	76.7 a-d
8	63.9 a	47.3 a-d	81.0 ab	80.2 a
9	43.7 i-m	41.7 c-k	67.0 c-g	64.7 c-d
10	46.3 f-e	37.7 f-m	51.3 j-o	82.7 a-d
11	41.3 k-n	38.0 f-m	56.0 f-m	66.7 a-d
Kat B9	51.3 c-h	45.3 a-g	75.7 a-d	78.7 a-d
GLP x 092	53.3 b-e	44.3 a-g	73.0 a-e	62.0 d
GLP 1004	57.0 bc	41.0 d-l	60.2 g-n	80.3 a-d
Okuodo	43.7 i-m	40.0 d-m	46.3 m-p	75.3 a-d
16	46.7 e-k	38.3 e-m	62.0 e-k	66.0 a-d
Kat B1	52.3 c-f	42.7 b-k	80.3 ab	89.3 abc
GLP 2	40.3 k-n	51.0 a	61.0 e-l	72.0 a-d
19	41.7 k-n	36.0 h-n	60.3 e-l	75.3 a-d
20	49.3 d-j	43.7 a-i	51.3 j-o	76.7 a-d
21	33.7o	39.0 e-m	51.7 i-o	77.7 a-d
22	59.3 ab	43.3 a-j	46.4 m-p	77.7 a-d
23	33.7 0	29.7 h	48.3 p	65.0 cd
24	42.3 k-n	33.3 lmn	56.3 f-m	65.3 bcd
Mbalaria	50.7 c-h	42.3 c-k	52.0 h-o	91.0 ab
26	41.7 k-n	47.7 a-d	49.0 j-p	91.7 a
27	45.9 g-l	44.0 a-h	65.7 c-h	81.7 a-d
28	42.7 j-m	32.0 mn	45.4 nop	84.3 a-d
SEQ 1001	64.0 a	40.0 d-m	66.1 d-j	75.0 a-d
SEQ 1004	50.3 c-i	49.8 abc	67.0 c-g	76.3 a-d
SEQ 1008	51.6c-g	40.0 d-m	60.7 e-l	82.7 a-d
SEQ 1012	52.4 c-f	49.7 abc	65.5 c-h	67.3 a-d
SEQ 1014	50.3 c-i	45.7 a-f	55.3 f-n	74.3 a-d
34	46.0 f-l	42.3 c-k	49.0 p	63.3 d
Ulonzo	45.3 g-e	45.7 a-f	78 abc	75.7 a-d
White Haricot	35.7 no	35.7 i-n	69.0 b-f	84.3 a-d
Mean	45.3	41.6	57.8	75.3
S.E	2.9	3.4	5.7	4.8
CV (%)	13.5	9.9	12.1	7.7

Means followed by the same letter in columns are not significantly different at 0.05 Probability level (DMRT).

Table 22. **Root dry weight (g plant^{-1}) means for 36 drybean genotypes measured at two occassions (15 DAE and 36 DAE) under water stress (WST) and non-stress (NST) treatments at Kiboko.**

	Root dry weight (g plant^{-1})			
	15 DAE		36 DAE	
Genotype	WST	NST	WST	NST
1	0.11 no	0.52 bc	0.71 d-j	1.56 b-g
2	0.21 f-j	0.38 h-k	1.14 a	1.95 a
3	0.25 efg	0.32 e-r	0.49 k-n	1.56 b-g
4	0.21 f-j	0.35 k-p	0.56 j-n	1.36 d-k
5	0.18 h-m	0.41 g-j	0.80 c-g	1.07 i-o
6	0.15 j-n	0.32 mx	0.55 j-n	1.00 j-o
7	0.14 lmn	0.35 k-p	0.44 mm	0.98 j-o
8	0.58a	1.12 a	0.94 bc	1.99 a
9	0.14 l-o	0.43 e-i	0.77 c-h	1.23 g-n
10	0.26 ef	0.46 d-g	0.63 g-k	1.03 i-o
11	0.12 mno	0.41 f-j	0.56 i-n	0.93 l-o
Kat B9	0.51 b	0.56 b	0.80 c-g	1.95 ab
GLP x 092	0.54 ab	0.43 e-i	0.74 d-i	1.39 d-i
GLP 1004	0.23 e-h	0.35 k-p	0.71 d-j	1.27 f-m
Okuodo	0.16 j-n	0.29 pqr	0.44 mn	0.94 k-o
16	0.33 cd	0.30 n-r	0.56 i-n	1.63 a-g
Kat B1	0.29 de	0.45 e-h	0.82 c-f	1.30 f-m
GLP 2	0.20 f-k	0.38 i-m	0.77 c-h	1.52 c-h
19	0.17 h-m	0.31 n-r	0.44 lmn	1.10 h-o
20	0.16 i-n	0.51 bed	0.64 f-k	0.78 o
21	0.18 h-m	0.47 c-f	0.62 h-l	1.32 e-m
22	0.17 i-m	0.33 l-q	0.45 lmn	1.32 e-m
23	0.08 o	0.20 s	0.25 o	0.81 no
24	0.17 h-m	0.29 o-	0.58 i-m	0.91 mno
Mbalaria	0.22 f-i	0.41 g-j	0.84 cde	1.72 a-e
26	0.19 g-l	0.40 g-j	0.44 mn	1.40 c-i
27	0.21 f-j	0.43 e-i	0.66 e-k	1.24 g-m
28	0.21 f-j	0.30 n-r	0.66 f-k	1.65 a-g
SEQ 1001	0.21 f-j	0.52 bc	1.05 ab	1.34 e-l
SEQ 1004	0.21 f-j	0.26 r	1.06	1.39 d-i
SEQ 1008	0.14 k-n	0.48 cde	0.86 cd	1.68 a-f
SEQ 1012	0.33 cd	0.64 a	0.94 bc	1.81 abc
SEQ 1014	0.35 c	0.48 cde	0.78 c-h	1.45 c-i
34	0.33 cd	0.35 j-o	0.40 n	1.04 i-o
Ulonzo	0.59 a	0.36 j-n	0.68 e-j	1.33 e-l
White Haricot	0.15 k-n	47.35	0.61 h-m	1.04 i-o
Mean	0.23	0.4	0.69	1.33
S.E	0.03	0.03	0.18	0.17
CV (%)	12.3	8.3	22.4	15.4

Means followed by the same letter in columns are not significantly different at 0.05 Probability level (DMRT).

4.3 Interrelationships between some physiological and morphological traits.

The correlation coefficients between indicators of plant water status (RWC, LWP) and days to 50% flowering (DTF), relative growth rates (RGR1 and RGR2) and root growth parameters (TRL and RDW) under water stress treatments are presented in Table 23. The RWC at seedling stage (15 DAE) in both seasons was positive and significantly correlated with RGR1 (r=0.58**, r=0.42**) and TRL monitored at 15 DAE (r=0.39**, r=0.29*). At the preflowering stage (22 DAE), RWC was positive and significantly correlated in both seasons with RGRI (r=0.40**, 0.33*) and TRL at 15 DAE (r=0.4**, r=0.36**). At flowering stage (29 DAE) RWC was positive and significantly correlated in both seasons with RGR2 (r=0.32*, r=0.28), RDW at 36 DAE (r=0.49**, r=0.38**), TRL at 15 DAE (r=0.28*, r=0.33*) and TRL at 36 DAE (r=0.40**, r=0.54**).

At seedling stage (15 DAE), LWP was positive and significantly correlated in both seasons with RDW at 15 DAE (r=0.58**, 0.44**), TRL at 15 DAE (r=0.36**, r=0.33*) and RGR1 (r=0.31*, r=0.49**) At preflowering stage (22 DAE), LWP was positive and significantly correlated in both seasons with RGRI (r=0.49 **, r=0.36**), TRL at 15 DAE (r=0.59 **, r=0 53**) and TRL at 36 DAE (r=0.31*, 0.42**) and RDW at 36 DAE (r=0.36**, 0.52**). .At flowering (29 DAE), LWP was positive and significantly correlated in both seasons with TRL at 36 DAE (r=0.56 **, r=0.61**) and only in one season with RGR2 (r=0.29*) and RDW at 36 DAE (r=0.32).

Days to 50% flowering (DTF) was negative and significantly correlated in both seasons with RWC at 29 DAE (r=-0.30*, r=-0.42**), RWC at 36 DAE (r=-0.29*, -0.31*), LWP at 22 DAE (r=-0.55**, r=-0.37**) andLWP at 29 DAE (r=-0.35**, -0.28*).

Table 23. **Matrix correlation coefficients between relative water content and leaf water potential and at four sampling episodes with some physiological traits under water stress treatment during January - March, 1996 (season 1) and May - July, 1996 (season 2) at Kiboko.**

	SEASON	DTF	RGR1	RGR2	RDW15	RDW36	TRL15	TRL36
RWC15	1	-0.04	0.58**	0.08	0.25	0.21	0.39**	-0.14
	2	0.06	0.42**	0.03	0.16	0.19	0.28*	0.01
RWC22	1	0.14	0.40**	0.02	0.19	0.46**	0.44**	0.13
	2	-0.19	0.33*	0.22	0.23	0.38**	0.36**	0.21
RWC29	1	-0.30*	0.24	0.32*	0.18	0.26*	0.28*	0.40**
	2	-0.42**	0.20	0.28+	0.23	0.38**	0.33**	0.54**
RWC36	1	-0.29*	0.20	0.29*	0.14	0.112	0.22	0.07
	2	-0.31*	0.26	0.12	0.11	0.19	0.16	0.10
LWP15	1	0.05	0.31*	0.16	0.15	0.22	0.36**	0.26
	2	0.125	0.49**	-0.13	0.24	0.11	0.33*	0.05
LWP22	1	-0.55**	0.49**	-0.21	0.16	0.36**	0.59**	0.31*
	2	-0.37**	0.36**	0.12	0.24	0.52**	0.53**	0.42**
LWP29	1	-0.38**	0.12	0.29*	0.22	0.32*	0.12	0.56**
	2	-0.28+	0.02	0.23	0.12	0.11	0.21	0.61**
LWP36	1	-0.14	0.24	-0.21	0.22	0.24	0.02	0.21
	2	-0.08	0.03	0.26	0.18	0.13	0.11	-0.02

+, *, **, Significant at P< 0.10, 0.05 and 0.01 respectively

RWC,Relative water content at 15, 22, 29 and36 DAE ; LWP, Leaf water potential at 15, 22, 29 and 36 DAE

DTF, days to 50% flowering; RGR1, relative growth rate between seedling and pre-flowering

RGR2, relative growth rate between pre-flowering and pod development; TRL15, taproot length at 15 DAE; TRL36, root length at 36 DAE.

RDW15, root dry weight at 15 DAE; RDW36, root dry weight at 36 DAE

4.4. Experiment III: Genetic analysis of indicators of plant water satus and of root growth.

4.4.1 Relative Water Content (RWC)

Parental and generations means for percent leaf relative water content (RWC) is presented in Table 24 for crosses P4 x P10 and P4 x P28. At pre-flowering (22 DAE) and pod development (36 DAE) growth stages, the mean RWC of P4 was significantly higher ($P<0.05$) than that of parent P10. The difference between the high and low value parents was 8.5 and 21.5% at 15 and 36 DAE, respectively. In cross P4 x P28, at pre-flowering (22 DAE) and flowering (36 DAE) growth stages, the mean RWC of parent P4 was significantly higher ($P<0.05$) than that of parent P28. A parental RWC difference of 18.1% and 33.2% was detected at 15 and 36 DAE, respectively. This data show that the parental differences were generally higher at 36 DAE than 22 DAE in both crosses. In cross P4 x P10 at 22 DAE the F1 mean was significantly higher ($P<0.05$) than all the generations and parental means and the mid-parent value. Conversely, the mean of the backcross to the higher value parent (F1 P4) was significantly lower than the parental and other generation means ($P<0.05$). The mean of the backcross to the lower value parent was similar to the parental means, the mid-parent value and the F2 mean. In this cross there was a tendency of a backcross to a high value parent to perform lower than the high value parent and vice versa at the seedling stage. At 36 DAE, the F1 and F2 means and the mean of the backcross to the high value parent, and the midparent value were similar. The mean of the backcross to the low value parent was low but similar to the low value parent mean. At the flowering stage, the backcross means tended to

skew towards their respective parental means. In the cross P4 x P28 at seedling stage (22 DAE), the F_1, F_2 mean and the mean of the backcross to the high value parent and the midparent value were similar. The backcross to high value parent (BC_1F_1) was also significantly lower than the high value parent. The mean of backcross to the low value parent (BC_2F_1) was significantly higher than the mean of the low value parent but not from the high value parent ($P<0.05$). At this stage of growth, the backcross to the low value parent tended to skew towards the high value parent. At 36 DAE, the F2 and the means of backcross to the high and low value parents were lower but not significantly different from the high value parent ($P< 0.05$). Again as at 22 DAE, there was a tendency for a mean of the backcross to a low value parent to skew towards a high value parent mean.

The mean square values of the genetic effects for RWC measured at 15 and 36 DAE are presented in Table 25. The mean square values for generation means were highly significant ($P<0.01$) in all crosses during all the sampling episodes. The mean square values for each genetic effect were converted to percentages in order to improve clarity in comparison within and among crosses and to assist in interpretation of the results. These values are presented in Table 26. In cross P4 x P10 at seedling stage (22 DAE), additive (d), additive x dominance (j) and dominance x dominance (l) interactions effects were highly significant ($P<0.01$) at pre-flowering (22 DAE) and accounted for 30, 42 and 27% of the variation in total gene effects, respectively. At pod development (36 DAE), additive (d) dominance (h) additive x additive (i) and dominance x dominance epistatic effects were highly significant ($P<0.01$), and accounted for 34, 20, 20, and 24%, of the variation in total gene effects, respectively (Table 26). In cross P4 x P28, only additive x dominance (j) epistatic

effects were highly significant ($P<0.01$) and contributed 83% of the total variation in gene effects at pre-flowering (22 DAE). At pod development (36 DAE), additive x dominance epistatic effects were more important and accounted for 70% of the variation in total gene effects. Small (14%) but highly significant dominance x dominace (l) gene effects was also detected.

Table 24. Means for midday relative water content (RWC) for generations and their parents in two dry bean crosses at pre-flowering (22 DAE) and at pod development (36 DAE) under water stress conditions at Kiboko in 1997.

	Cross			
	P4 x P10		P4 x P28	
	22 DAE	36 DAE	22 DAE	36 DAE
P_1	76.86 b	75.68 a	76.86 a	75.68 a
P_2	68.38 c	54.20 c	58.08d	42.44 c
Mid parent	72.62	64.94	67.47	59.06
F_1	86.07 a	63.40 b	67.08 c	66.59 b
F_2	67.34 c	67.70	70.97 abc	68.13 ab
BC_1 (F_1 P_1)	58.43 d	65.16 b	67.35 bc	68.36 ab
BC_2 (F_1 P_2)	71.70 bc	49.93 c	73.19 ab	74.70 a
LSD (0.05)	5.1	6.3	5.92	7.62

Means followed by the same letter in columns are not significantly different at 0.05 Probability level (LSD).

where,

- P1 = high value parent [4 (Ex-Embu)]
- P2 = low value parent [(10 (Ex-Nyeri) and 28 (Ex-Kisii)]
- Mid parent = (high value parent + low value parent) ÷ 2
- F_1 = the first generation of a cross
- F_2 = the second filial generation obtained by self-fertilization
- BC_1 F_1 = the cross of the first generation of a cross (F_1) to the high value parent
- BC_2 F_1 = the cross of the first generation of a cross (F_1) to the low value parent

Table 25. **Mean Squares from analysis of variance for midday relative water content (RWC) from four generations and their parents at pre-flowering (22 DAE) and at pod development (36 DAE) sampling episodes at Kiboko in 1997.**

Source of variation		Mean squares			
		P4 x P10		P4 x P28	
		22 DAE	36 DAE	22 DAE	36 DAE
Replication	2	9.52	33.27	14.65	1.31
Generation	5	1317.30**	1305.99**	626.50**	2204.41**
d	1	264.14**	348.08**	51.22	60.36
h	1	2.30	208.88**	1.18	52.60
i	1	10.20	106.05**	0.97	23.19
j	1	368.06**	24.23	278.47**	632.69**
l	1	243.08**	250.13**	4.70	130.41*
Error	10	134.93	158.22	105.93	175.58
CV (%)		5.1	6.3	4.7	6.4

*, ** significant at $P < 0.05$ and 0.01 levels, respectively.

where,

- d = additive effects
- h = dominance effects
- i = additive x additive interaction effects
- j = additive x dominance interaction effects
- l = dominance x dominance interaction effects

Table 26. **Percent variability due to the gene effects within each dry bean cross for midday relative water content (RWC) at preflowering (22 DAE) and pod development (36 DAE) sampling episodes at Kiboko in 1997**

Source of variation	Percent variability due to gene effects			
	P4 x P10		P4 x P28	
	22 DAE	36 DAE	22 DAE	36 DAE
d	30**	34**	15	7
h	0	20**	0	6
i	1	20**	0	3
j	42**	2	83**	70**
l	27**	24**	2	14**

*, ** significant at P< 0.05 and 0.01 levels, respectively.

where,

- d = additive effects
- h = dominance effects
- i = additive x additive interaction effects
- j = additive x dominance interaction effects
- l = dominance x dominance interaction effects

4.4.2 Leaf Water Potential

The data for parental, F_1, F_2 and back cross generations means for two crosses are presented in Table 27. In cross P2 x P20 the percent difference (calculated on the basis of a higher parent mean) of 31.1 and 29.5% at 15 and 36 DAE, respectively were obtained. In cross P4 x P20 there was a difference of 75.6 and 72.7% at 15 and 36 DAE, respectively. The parental differences within a cross at the two sampling episodes were almost similar. In cross P2 x P20, the F_1 mean was lower and significantly different from the F_2 mean ($P<0.05$) but higher than mid-parent value at both 15 and 36 DAE. The mean of back cross to the high value parent was significantly higher than the mean of the recurrent parent ($P<0.05$) at both development stages. Similarly, the mean of the back cross to the low value parent was significantly higher than the mean of the recurrent parent ($P<0.05$). This data show that high LWP is fixable in this cross at all the stages of growth. In cross P4 x 20 at 15 the F1 mean was lower but not significantly different from the F_2 mean but significantly higher than the F_2 mean ($P<0.05$) at 36 DAE. At both development stages, the F_1 mean was higher than the mid parent value. The mean of the backcross to the high value was significantly higher than the means of all the other generations but similar to the recurrent parent ($P<0.05$) at both development stages. The mean of the back cross to the lower parent was significantly higher than the mean of the recurrent parent ($P<0.05$) at both sampling episodes. There was also a tendency for the generation means to skew towards the mean of the high value parent. The backcross mean to the high value parent in both crosses were higher than the high value parent mean, indicating that high LWP was fixable in the early generations.

The mean square values of the gene effects are presented in Table 28. The mean square values for generation means were highly significant ($P<0.01$) at both developmental stages in each cross. The mean squares for LWP were also converted for ease of comparison and interpretation to percent variability due to gene effects. Their values are presented in Table 29. In cross P2 x P20, additive (d), additive x additive (i) and additive x dominance (j) interaction effects were highly significant ($P< 0.01$) and accounted for 73, 8 and 13% of the variation in gene effects, respectively at pre-flowering (22 DAE). At pod development (36 DAE), additive (d), additive x additive (j) and additive x dominance (i) interaction effects were significant and accounted for 93, 4 and 3% of the genetic variability, respectively. In cross P4 x P20,. additive (d) and dominance x dominance (l) interaction effects were significant and accounted for 56 and 30% of the variation in gene effects, respectively. In cross P4 x P20 at pre-flowering (22 DAE). However, at pod development (36 DAE), only additive (d) gene effect was highly significant ($P<0.01$) and accounted for 91% of the genetic variability.

Table 27. **Means for midday leaf water potential (LWP) for generations and their parents in two dry bean crosses at 22 and 36 DAE under water stress conditions at Kiboko in 1997.**

	Cross			
	P2 x P20		P4 x P20	
Generation	22 DAE	36 DAE	22 DAE	36 DAE
P_1	-0.11 a	-0.62 b	-0.12 a	-0.66 b
P_2	-0.45 d	-1.12d	-0.45 d	-1.12 c
Mid parent	-0.28	-0.87	-0.29	-0.89
F_1	-0.19 b	-0.65 bc	-0.13 a	-0.88 bc
F_2	-0.17 b	-0.55 a	-0.21 b	-0.58 a
BC_1 (F_1 P_1)	-0.10 a	-0.53 a	-0.10 a	-0.50 a
BC_2 (F_1 P_2)	-0.31 c	-0.63 c	-0.32 c	-0.77 b
LSD (0.05)	0.03	0.09	0.07	0.24
CV (%)	5.6	14.8	8.1	18.6

Means followed by the same letter in columns are not significantly different at 0.05 Probability level (LSD).

where,

- P1 = high value parents[2 (Ex-Kitui) and 4 (Ex-Embu)]
- P2 = low value parent [20 (Ex-Nyeri)]
- Mid parent = (high value parent + low value parent) ÷ 2
- F_1 = the first generation of a cross
- F_2 = the second filial generation obtained by self-fertilization
- BC_1 F_1 = the cross of the first generation of a cross (F_1) to the high value parent
- BC_2 F_1 = the cross of the first generation of a cross (F_1) to the low value parent

Table 28. **Mean Squares from analysis of variance for leaf water potential (LWP) from four generations and their parents at pre-flowering (22 DAE) and at pod development (36 DAE) sampling episodes at Kiboko in 1997.**

Source of variation	Df	Mean squares			
		P2 x P20		P4 x P20	
		22 DAE	36 DAE	22 DAE	36 DAE
Replication	2	0.001	0.001	0.028	0.002
Generation	5	0.109**	0.844**	0.097**	0.271**
d	1	0.028**	0.068**	0.027**	0.070**
h	1	0.001	0.000	0.001	0.003
i	1	0.003**	0.003*	0.001	0.000
j	1	0.005**	0.002*	0.005	0.004**
l	1	0.001	0.000	0.014	0.000
Error	10	0.003	0.003	0.023	0.017
CV (%)		5.1	4.7	6.3	6.4

*, ** significant at P< 0.05 and 0.01 levels, respectively.
where,

- d = additive effects
- h = dominance effects
- i = additive x additive interaction effects
- j = additive x dominance interaction effects
- l = dominance x dominance interaction effects

Table 29. **Percent variability due to the gene effects within each dry bean cross for midday Leaf water potential (LWP) at pre-flowering (22 DAE) and pod development (36 DAE) sampling episodes at Kiboko in 1997**

Source of variation	Percent variability due to gene effects			
	P2 x P20		P4 x P20	
	22 DAE	36 DAE	22 DAE	36 DAE
d	73**	93**	56**	91**
h	3	0	2	4
i	8**	4*	2	0
j	13**	3*	10	5
l	3	0	30*	0

*, ** significant at P< 0.05 and 0.01 levels, respectively.

where,

- d = additive effects
- h = dominance effects
- i = additive x additive interaction effects
- j = additive x dominance interaction effects
- l = dominance x dominance interaction effects

4.4.3 Taproot length

The mean taproot lengths for cross P2 x P23 and cross P8 x P23 are presented in Table 30. There were significant differences between the parental means ($P<0.05$) in both crosses. Parent 2 and parent 8 were the high value parents in cross P2 x P23 and P8 x P23, respectively, while parent 23 was the low value parent. In cross P2 x P23, the F_1 mean was similar the F_2 mean but significantly higher than the mean of the low value parent. The F_1 mean was lower than the mid parent value. The mean of the back cross to the high value parent (BC_1F_1) in cross P2 x P23 was significantly lower than the recurrent parent mean but similar to the F_1, F_2 and the low value parent means ($P<0.05$). However, the mean of the back cross to the low value parent was lower but not significantly different from the mean of the recurrent parent ($P<0.05$). In cross P8 x P23, the F_1 mean was similar to the F_2 mean and the midparent value. The mean of the backcross to the higher value parent and the mean of the back cross to the low value parent were similar to the means of their recurrent parents ($P<0.05$). In this cross, there was a strong tendency for back cross means to regress towards their parental means. The mean squares of gene effects for the two crosses are presented in Table 31. The generation mean square values were highly significant ($P<0.01$) and higher for cross P2 x P23 than for cross P8 x P23. Percent variability due to gene effects are presented in Table 32. In cross P2 x P23 additive x dominance (j) and dominance x dominance (l) interaction gene effects were highly significant ($P<0.01$) in both crosses and accounted for 66 and 21% of the total variability, respectively. In cross P8 x P23, only additive x dominance (j) gene effects were and highly significant ($P<0.01$) and accounted for 60% of the total variability gene effects.

4.4.4 Root Dry Weight

Table 30 presents data for the parental, F_1, F_2 and back cross means for the two bean crosses. Significant differences between means were found between the high and low value parents ($P<0.05$) in both crosses. The percent difference (calculated on the basis of a high value parent) in cross P2 x P23, and cross P8 x P23 were 65,0 and 67.9%, respectively.

In cross P2 x P23, the F_1 mean was significantly higher than the F_2 mean ($P<0.05$) and about two times higher than the mid parent value. The F_2 mean was higher and significantly different from the mean of the higher value parent ($P<0.05$). The mean of the back cross to the high value parent was significantly lower than the mean of the recurrent parent. Conversely, the mean of the back cross to the low performing parent was significantly higher than the mean of the recurrent parent ($P<0.05$) but similar to the F1 mean.

The F1 mean in cross P8 x P23 was similar to the mid parent value but significantly higher than the F2 mean value. The mean of the back cross to the high value parent was similar to the F2 mean but significantly lower than the mean of the recurrent parent ($P<0.05$). However, the mean of the back cross to the low value parent was low but similar to the mean of the recurrent parent.

The mean square values of gene effects are presented in Table 31 for the two crosses. The generation mean square values were highly significant ($P<0.01$) and of similar magnitude in both crosses. The mean square values of the gene effects converted to percentages are shown in Table 32. In both crosses, only additive x dominance (j) interaction gene effects were highly significant ($P<0.01$) and contributed 81 and 62% of the total variability in cross P2 x P23 and P8 x P23, respectively. A low but highly significant dominance x dominance (l)

interaction effect ($P<0.01$) was detected in cross P8 x P23, and contributed 25% of the variability. These results suggest that this character is primarily controlled by complex gene action.

Table 30. Means for taproot length (TRL) and for root dry weight (RDW) for four generations and their parents in two crosses at 36 days after emergence under water stress field conditions at Kiboko in 1997.

Generation	Cross			
	P2 X P23		P8 X 23	
	TRL (cm.)	RDW (g plant^{-1})	TRL (cm.)	RDW (g plant^{-1})
P_1	71.9 a	1.190b	66.4a	1.300a
P_2	46.5cd	0.417d	46.5c	0.417d
Mid parent	59.2	0.804	56.5	0.859
F_1	53.9b	1.547a	55.5b	0.987b
F_2	51.3bc	1.097bc	51.4b	0.703c
BC_1 (F_1 P_1)	43.0bc	0.920c	62.7a	0.737c
BC_2 (F_1 P_2)	51.6d	1.427a	46.1c	0.410b
LSD (0.05)	5.6	0.217	4.4	0.148
CV (%)	5.8	10.7	4.4	10.9

Means followed by the same letter in columns are not significantly different at 0.05 Probability level (LSD).

where,

- P1 = high value parent [2 (Ex-Kitui) and 8 (Ex-Kirinyaga)]
- P2 = low value parent [23 (Ex-Meru)]
- Mid parent = (high value parent + low value parent) ÷ 2
- F_1 = the first generation of a cross
- F_2 = the second filial generation obtained by self-fertilization
- BC_1 F_1 = the cross of the first generation of a cross (F_1) to the high value parent
- BC_2 F_1 = the cross of the first generation of a cross (F_1) to the low value parent

Table 31. Mean Squares from analysis of variance for taproot length (TRL) and root dry weight (RDW) from four generations and their parents pod development (36 DAE) growth stage at Kiboko in 1997.

Source of variation	df	Mean squares			
		P2 X P23		P8 X 23	
		TRL	RDW	TRL	RDW
Replication	2	0.42	0.003	4.13	0.040
Generation	5	303.70**	0.486**	212.86**	0.352**
d	1	22.90	0.084	85.47	0.067
h	1	45.35	0.107	22.45	0.011
i	1	31.73	0.012	18.18	0.034
j	1	484.63**	0.868**	194.05*	0.503**
l	1	156.80*	0.005	1.89	0.204**
Error	10	181.64	0.443	388.45	0.159
CV (%)		8.0	19.2	11.4	16.6

*, ** significant at P< 0.05 and 0.01 levels, respectively.

where,

- d = additive effects
- h = dominance effects
- i = additive x additive interaction effects
- j = additive x dominance interaction effects
- l = dominance x dominance interaction effects

Table 32. **Percent variability due to the genetic effects within each dry bean cross for mean taproot length (TRL) and root dry weight (RDW) for four generations and their parents in two crosses at 36 days after emergence under water stress field conditions at Kiboko in 1997.**

Source of variation	Percent variability due to the gene effects			
	P2 x P23		P8 x P23	
	TRL	RDW	TRL	RDW
d	3	27	8,	8
h	6	7	10	1
i	4	6	1	4
j	66**	60**	81**	62**
l	21**	0	0	25**

*, ** significant at P< 0.05, 0.01 levels, respectively.

where,

- d = additive effects
- h = dominance effects
- i = additive x additive interaction effects
- j = additive x dominance interaction effects
- l = dominance x dominance interaction effects

CHAPTER V
5.0 DISCUSSION

5.1.1 Response of some physiological and morphological traits to water stress

Results from this study showed consistent genotypic differences in the response of morphological and physiological traits of drought resistance to water stress.

There was genotypic variability in days to flower both under water stress and nonstress treatments in both seasons. Earliness in flowering was observed both in genotypes that had high plant water status (for example Ulonzo, GLP 1004, KAT B1) and in those that had low plant water status (for example 10 (Ex-Nyeri), 11 (Ex-Kisii), 28 (Ex-Kisii), and 21 (Ex-Kiambu) under water stress at midday. Earliness in flowering was also negatively correlated with the indicators of plant water status, suggesting that majority of the genotypes tested did not posses other mechanisms of drought resistance.

Earliness in beans is most advantageous drought escape mechanism where soil moisture is adequate early in the season but declines rapidly as the season progresses (Njugunah *et al.* 1981; Acosta *et al.*, 1989; White and Singh, 1991). Earliness in flowering has also been recommended as a selection criterion for adaptation of beans to arid and semi-arid zones (Fischer and Turner, 1978).

Earliness in flowering was also observed in genotypes with low RWC and LWP values under water stress and collected from the high rainfall environments for example, 10 (Ex-Nyeri), 11 (Ex-Kisii), 28 (Ex-Kisii), and 21 (Ex-Kiambu). These observations suggest that over the years, farmers in the higher rainfall areas probably selected for genotypes that are early in flowering to escape water stress, which occasionally occur in seasons of prolonged

droughts. These genotypes are also suitable for growing during the short seasons that have high risks of crop failure.

Genotypic differences in leaf relative water content (RWC) and leaf water potential (LWP) were detected both at predawn and midday at the four sampling episodes which corresponded with seedling (15 DAE), preflowering (22 DAE), flowering (29 DAE) and pod development (36 DAE) sampling episodes in both seasons. The predawn RWC and LWP values were always higher than the midday values in both water stress and nonstress treatments. The decrease in the midday values under the nonstress treatment may be attributed to a rapid increase in atmospheric evaporative demand due to high ambient temperature and low relative humidity (Hale and Orcutt, 1987); while under the water stress treatment, the decrease in these values at midday was due to the above factors including tissue water stress arising from soil water deficits (Kramer, 1983). Plant moisture absorption lags always behind loss during periods of peak evaporative demand (Turner, 1979). The RWC and the LWP rose to their highest levels at predawn due to reduction in transpiration later in the day while absorption continues, thereby allowing leaves to recover turgor at night. The predawn values in this study may reflect the genotypic differences in capacity to rehydrate overnight and as with rice (O'Toole and Chang, 1979), the predawn values may be a good indicator of development of the genotypic root system.

As the season progressed, from 15 DAE to 36 DAE, a general decline in the RWC and LWP values was also observed. Distinct genotypic differences in RWC and LWP values were observed after seedling stage (15 DAE) in both seasons. This observation may be attributed to the adequate availability of the stored soil moisture in the soil profile early in the growth cycle

which allowed relatively less water stress compared to the later sampling episodes. Under water stress, genotypes 2 (Ex-Kitui), 4 (Ex-Embu) 8 (Ex-Kirinyaga), KAT B1, KAT B9, GLP x 92 and Ulonzo maintained relatively higher RWC and LWP values and greater root growth compared to other genotypes. These genotypes maintained relatively high plant water status by increasing water uptake. The genotypes achieved it by developing a large deep root system that efficiently extracted soil water as evidenced by a greater increase of taproot length, rather than the root density as the season progressed from 15 DAE to 36 DAE, particularly in the nonstress treatment. During the early stages of water deficits, plants usually respond by increasing supply of stored soil moisture into the leaves to meet evaporative demand.

Results from this study show that at seedling stage (15 DAE), taproot length was enhanced while the root dry weight decreased under water stressed treatment compared to the nonstress. The generally enhanced taproot length under the water stress conditions could be attributed to a need for rapid root penetration, rather than root density during the early growth stages. Reduced growth of the taproot under non water stress conditions could be attributed to poor root aeration, arising from saturation of soil with water that reduces oxygen supply to the root (Kramer, 1983). However, as the season progressed, the growth of taproot length and root dry weight was reduced under water stress. These results appear to show that rapid taproot growth in the early growth stage is desirable under water stress. These observations agree with the findings of Runkulatile *et al.* (1993). They reported that bean varieties adapted to low rainfall areas, for example Ulonzo and GLP x 92, had faster downward rooting ability compared to those adapted to the high rainfall areas. Similar observations have also been reported in other drought resistant pulses for example, in cultivars of French beans (Sangakkara, *et al.*, 1996), field bean

and field peas (Grzesiak *et al.*, 1997). This adaptation mechanism permits plants to maintain high plant water status by increased absorbtion from the wet lower soil profiles.

Incidentally, majority of genotypes that had high RWC and high LWP values under water stress, were of indeterminate growth habit (type II) compared to the genotypes of determinate growth habit (type I) suggesting that indeterminate genotypes maintain higher plant water status, and hence, more drought resistant than the determinate genotypes. Turner (1979) has ascribed this phenomenon to adaptation of the genotypes to wide developmental plasticity under water stress. These genotypes also had well developed root growth, which may have maintained water uptake from the lower soil profile, or the plants reduced their transpiration rates as the severity of water stress increased.

The response of growth to water stress, as measured by the relative growth rate (RGR) was monitored in two harvest occasions: from planting upto flowering and from flowering up to pod development. In both occasions, the RGR was generally reduced in all the genotypes under water stress compared to the nonstress treatment. The RGR values monitored in the first and second harvesting occasions were generally similar, but lower under the water stress compared to the nonstress treatment. The genotypes that maintained high RGR values under water stress are also those that had high plant water status as measured by RWC and LWP. This was an indication of their drought resistance arising from mechanisms of adaptation

Maintenance of high plant water status in these genotypes under water stress at all the sampling episodes could also be attributed to other factors, in addition to efficient water uptake by the roots. These genotypes possibly restricted water loss by stomatal control or reduction of solar radiation intercepted by the plants through paraheliotropism (Parsons, 1982). Another

possible drought mechanism that allow a plant to maintain a high plant water status under progressive water deficits is by lowering tissue osmotic potential (Turner, 1979), a process called osmotic adjustment (Morgan, 1980a; Blum, 1988) or osmoregulation (Morgan, 1983). This drought adaptation mechanism has also been reported in Ulonzo and GLPX92 (Runkulatile *et al.*, 1993) and other pulses such as chickpea, lentils, faba beans, field peas, grass peas and lupins (Turner *et al.*, 1996); and in sorghum (Morgan, 1980a; Morgan, 1984; Blum, 1988; and Omanya *et al.*, 1996).

RGR was generally reduced by water deficits in all the genotypes. As the soil water potential at the root/soil interface becomes limiting, the plants respond by restricting their transpiration activities by control of water loss to the atmosphere (Turner, 1979). This can be achieved by reducing transpiration through an increase in stomatal and cuticular resistance, or a reduction in the evaporative surface (leaf area). These responses usually lead to a reduction in photosynthetic activity of the plant. Drought resistant genotypes are less affected compared to those that are susceptible. This phenomenon was ably demonstrated whereby the genotypes which had higher tissue leaf water status under water stress maintained relatively higher RGR values compared to those genotypes which had low leaf water status. These observations agree with those of Costa *et al.*, (1997) who found that lower RGR of dry beans arose from a reduced photosynthetically active area of the plant when grown under water stress conditions. Results from interrelationship analysis also indicated that under water stress, between seedling (15 DAE) and flowering (29 DAE), RWC and LWP were positively correlated with taproot length at 15 DAE and RGR before flowering. At flowering (29 DAE), RWC and LWP was correlated with RGR after flowering, root dry weight and taproot length. These results appear

to suggest that under water stress, between seedling and flowering, enhanced RGR arises from well developed taproot length that maintains water uptake, resulting in maintenance of an optimum leaf water status that maintain the photosynthetic activity of plant. However, between flowering and pod development, both taproot length and root density appear to maintain water uptake, probably, by increasing the root volume that explores the soil profile in search of the tightly bound soil water as the water deficit increases (Kramer, 1983).

Days to flower were negatively correlated with both indicators of plant water status in both seasons, generally suggesting that under water stress earliness in flowering was associated with a high plant water status.

When comparing a large number of genotypes and selecting from large populations, the measuring techniques must be simple and faster. The RWC method may be appropriate in dry beans because the measuring time is short and the required equipment are simple and cheap.

The results of this study suggest that rapid root growth is a desirable trait that may be included in a dry bean breeding program for development of cultivars adapted to water stress environments. Longer roots explore the soil profile better, hence maintaining a balance between transpiration demand and water absorption.

Various dry bean genotypes possessed drought resistance mechanisms as measured by plant water status, growth rate, earliness in flowering and root growth development. A superior genotype in this respect could perhaps be developed for semi-arid areas of Eastern Kenya by intercrossing these genotypes. For example, the early flowering genotypes could be intercrossed with those genotypes that had well developed root growth under conditions of soil water deficits. This could fortify drought escape arising from earliness with other mechanisms

of drought resistance thereby reducing the risks of crop failure where rainfall is inadequate and distribution is erratic, a common feature in the semi-arid areas.

These inherent mechanisms of adaptation to drought stress (earliness and maintenance of high plant water status) may be enhanced by using improved cultural and agronomic practices that reduce the onset of internal plant water stress, rate of progression of water deficits in the soil, severity and duration of drought. These practices include plant spacing and soil moisture conservation practices such as terracing of the farms, ridging of furrows before planting and mulching.

5.1.2 Genetic analysis of some physiological traits under water stress

The mode of inheritance of RWC, LWP, taproot length (RL) and root dry weight (RDW) in dry beans was examined under moisture stress conditions. These traits are associated with drought resistance. Knowledge of the mode of inheritance may hasten genetic advancement when breeding for drought resistance in beans.

At pre-flowering stage (22 DAE) examination of the significant partitioned genetic effects suggest that additive (d), additive x dominance (j), and dominance x dominance (l) epistatic effects largely influenced RWC in cross P4 x P10 and contributed 30, 42 and 27% of the total genetic effects, respectively. Only additive x dominance (j) epistatic effects (83%) were significant ($P<0.01$) in cross P4 x P28. At pod development (36 DAE), more epistatic effects were observed. In cross P4 x P10, the additive (d), dominance (h), additive x additive (i) and dominance x dominance (l) epistatic effects were significant and accounted for 34, 20,

20, and 24% of the total genetic effects, respectively while in cross P4 x P28, additive x dominance (i) (70%) and dominance x dominance (l) (14%) epistatic effects were significant. These results suggest that similar genes or alleles influence this trait at various growth stages and that the gene effects are cross specific. The results also suggest that simple selection procedures will not be effective in selecting for high midday RWC under moisture stress due to the presence of the non-fixable gene effects and possibly genetic linkages. It is suggested that intercrossing and following bulk population of breeding procedures that exploit both the additive and non-additive gene effects, thereby increasing the possibility of more gene combinations may be useful in improving this trait in dry bean.

Additive gene effects in both crosses predominantly influenced the inheritance of midday leaf water potential both at pre-flowering (22 DAE) and pod development (36 DAE) sampling episodes. In cross P2 x P20, additive (d) gene effect was significant and constituted 73% of the total variation. Small but significant ($P<0.01$) additive x additive (8%) and additive x dominance(13%) epistatic effects were also detected. In cross P4 x P20, moderate additive gene effect (56%) was also detected while small dominance x dominance (30%) epistatic effects was detected.

At pod development (36 DAE), midday LWP was highly conditioned by additive gene effects and contributed 93 and 91% of the total variability of gene effects in cross P2 x P20 and cross P4 x P20, respectively. The presence of large components of the additive effects suggest that rapid advance through pedigree method of breeding and early generation selection may result in accumulation of favourable alleles for this trait. The use of midday LWP under water stress may be of value in dry-bean breeding programmes as an indicator of drought

resistance. Evaluation and selection between pre-flowering and pod development may be more efficient because additive effects are highly predominant. These results also indicate that midday leaf water potential can be easily selected for in the early generations of breeding. Pedigree breeding and back cross breeding methods may be advantageous in this case.

The inheritance of taproot length and root dry weight were predominantly controlled by epistatic effects. For example, for taproot length, additive x dominance (j) epistatic effects contributed 66% and 81% of the total genetic effects in cross P2 x P 23 and cross P4 x P23, respectively. In cross P2 x P 23, small but significant dominance x dominance (l), epistatic effects (21%) were found. Root dry weight was also predominantly controlled by additive x dominance (j) epistatic effects and constituted 60% and 62% of the total genetic effects in cross P2 x P 23 and cross P4 x P23, respectively. Small but significant dominance x dominance (l) epistatic effects (25%) were detected in cross P8 x P 23. These results suggest that breeding and selection procedures that utilise epistatic effects may be designed to improve root length and root dry weight. For improvement to be realised, several generations of intermating and delayed selection to later generations may be advantageous to break the epistatic effects. Results from an experiment by Fawole *et al.*, (1982) showed that in four crosses, dominance effects were more important, while additive effects were more important in two crosses. Pedigree or inbred-backcross and their alternative breeding methods were suggested by White and Singh (1991) for introducing deep roots from donor parents into desirable recipient cultivars as sources of drought tolerance. The genetic analyses in this study generally detected previously unreported genetic effects of the measured traits in beans.

5.2 Recommendations for Future Research

It is recommended that:

1. The genotypes studied should be investigated further to confirm drought resistance in terms of yields and yield stability including the relationships between the physiological drought selection indicators and crop yield.

2. The progenies of the crosses included in these studies should be advanced beyond the F2 generation to establish heritability of the traits. This will confirm if the traits are fixable and that hybridisation can transfer the traits to commercial cultivars, establish the possibility of pyramiding the desirable genes and development of drought resistant cultivars through multiple selection of drought resistance traits.

3. Laboratory and glasshouse studies of the traits should be conducted and the results correlated with those from the field studies. This will ensure that those traits that can be rapidly and cheaply evaluated in the laboratory and glasshouse could be used to screen large number of genotypes within a short period at a low cost. There is also need to thoroughly evaluate seed yield of the genotypes with the superior drought resistance traits.

3. Currently, developments in molecular genetics are providing new knowledge of genes at the cellular, chromosomal and DNA levels. It is therefore recommended that studies be done to develop knowledge of molecular action and use of suitable markers associated with drought resistance parameters. This may enable breeders to improve breeding and selection more accurately and rapidly, compared to conventional methods.

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APPENDIX

Appendix. 1. Monthly mean minimum and mean maximum temperature (^{0}C), rainfall, and applied irrigation at Kiboko during season 1 and season 2.

Month	Rainfall mm) (	Rain days	Irrigation¶ (mm)		Av. Max. (0C)	Av. Min. (0C)	Monthly Mean (0C)
1996			**Season 1**				
			WS‡	**NS**			
January	31.0	4	67.2	118.0	33.4	17.6	25.5
February	59.0	4	36.8	71.4	33.7	18.3	26.0
March	53.4	5		20.1	33.6	19.5	25.5
April	51.4	4			32.5	17.4	25.0
Total WS			194.4				
Total NS				312.4			
1996			**Season 2**				
			WS	**NS**			
May	34.8	3	54.3	97.3	31.2	16.6	23.9
June	3.5	1	93.7	126.1	28.9	15.1	22.0
July	1.0	1	32.8	42.4	27.8	14.4	21.1
August	0.0	0	33.5		288	140	21.4
September		0	56.7		31.0	16.8	23.9
October	0.0	0	11.4		32.7	17.2	25.0
Total WS			186.3				
Total NS				304.5			
1997			**Off season**				
June	2.0	1	129.1		29.5	15.1	22.3
July	0.0	0	124.6		29.5	13.3	21.4
August	0.0	0	98.5		30.5	13.7	22.1
September	0.0	0	44.3		31.9	15.7	23.8
October	26.2	5	51.0		31.1	17.8	24.5

¶ water applied by irrigation was estimated using catch cans placed at an equidistance of 3 metres.

‡, WS = water stressed tretment; NS = nonstressed tratment.

Appendix 2. RGR mean squares from analysis of variance measured between seedling and pre flowering and between pre-flowering and pod development under water stress and nonstress treatments for two seasons at Kiboko.

Source of variation	df	Mean Squares	
		RGR1	RGR2
Season	1	0.009	0.002
Rep (Season)	2	0.010	0.010
Irrigation	1	0.112**	0.065
Irrigation * Season	1	0.002	0.005
Error (a)	2	0.001	0.015
Genotype	35	0.629**	0.882**
Genotype * Irrigation	35	0.651**	0.346**
Genotype * Season	35	0.111	0.100
Genotype x Season x Irrigation	35	0.010	0.001
Error (b)	140	0.040	0.050

***, ** significant at P< 0.05, 0.01 levels, respectively.**

Appendix 3. Taproot length (cm) and root dry weight (g plant-1) mean squares from combined analysis of variance of 36 dry bean genotypes measured at two occassions (15 DAE and 36 DAE) for two seasons under water stress (WS) and nonstress (NS) treatments at Kiboko.

Source of variation	df	Mean squares			
		Root length (cm.)		Root dry weight (g/plant)	
		15 DAE	29 DAE	15 DAE	29 DAE
Season	1	5732.7	8456.5	112.6	345.7
Replication (season)	3	4623.1	5357.8	98.7	297.4
Irrigation	1	5816.3**	7338.4**	107.8**	236.8*
Season x irrigation	1	1745.3	2198.9	34.6	112.6
Error (a)	3	1123.5	1534.2	28.7	87.4
Genotype	35	266.5**	525.4**	122.5**	348.6**
Genotypexirrigation	70	163.3**	386.9**	82.6*	127.4*
Genotype x season	35	145.6**	456.3**	49.6**	109.7**
Genotype x season x irrigation	35	128.4**	116.1	22.3	67.4**
Error (b)	144	28.1	68.4	12.4	22.1

*, ** significant at $P < 0.05$, 0.01 levels, respectively

Appendix 4. Mean Mass Water Content Measured gravimetrically (dry soil basis) at Kiboko soil sampled at 36 DAE in season 1 and season 2

	Non-Stress		Water Stress	
	% water content (dry soil basis)			
Depth (cm)	Season 1	Season 2	Season 1	Season 2
1-15	15.8	13.6	3.8	3.6
16-30	16.3	14.0	7.9	7.3
31-45	18.4	15.5	9.6	8.7
46-60	20.0	16.6	11.1	10.0
61-75	18.5	19.3	12.6	11.4
76-90	22.5	20.1	14.6	16.5