

USE OF PATH COEFFICIENT ANALYSIS IN IDENTIFICATION
OF TRAITS ASSOCIATED WITH WATER USE EFFICIENCY IN DROUGHT
TOLERANT WHEAT GENOTYPES.

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THESIS

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DECLARATION

This is my original work and has not been presented for a degree in any other University

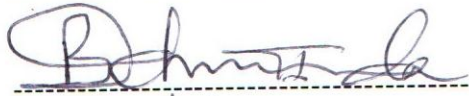
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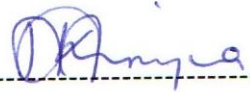
This thesis has been submitted for examination with our approval as University Supervisors.

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DEDICATION

Dedicated to my wife Sylvia and children Collins, Lorine and Grace.

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ABSTRACT

About one third of the developing world's wheat area is located in environments that are regarded as marginal for wheat production because of drought, heat and soil problems. Nearly one-third of the area planted to bread wheat and about three fourths of the area planted to durum wheat suffer from drought stress during the growing seasons. Despite these limitations, the world's dry and difficult cropping environments are increasingly crucial to food security in the developing world. Worldwide, investment in irrigation infrastructure has been reported to fall continually, while population growth and demand for wheat are rising. Gains in wheat productivity in marginal environments are important because it is unlikely that increased productivity in the favourable environments will be sufficient to meet the projected growth in demand for wheat from the present to 2020. In this regard, this study was aimed at establishing an indirect selection method for drought tolerance in wheat genotypes through traits associated with water use efficiency (WUE). An experiment was conducted under rain shelter for two seasons (2001-2002) with six cultivars (Duma, Ngamia, Chozi, Kwale, Mbuni and Pasa) tested under two moisture regimes (High and low moisture regimes). The experiment was a randomized complete block design (RCBD) with split arrangement of the treatments. Moisture regime was assigned as the main plot and cultivars as the sub-plot. An analysis of variance was carried out on combined season data. The data was further subjected to correlation and path coefficient analyses. The key parameters measured during the study included evapo-transpiration (ET), WUE, grain yield. Measurements for ET involved the summation of the change in soil moisture storage and the amount of irrigation applied during the season, whereas WUE was determined as a ratio of grain yield to ET.

The genotypes tested significantly differ in their water use efficiency (WUE) under both low and high moisture condition. Drought tolerant wheat cultivars (Duma, Ngamia and Chozi) had significantly higher WUE under moisture stress than the drought susceptible cultivars (Kwale, Mbuni and Pasa). The WUE of drought tolerant wheat cultivars (Duma, Ngamia and Chozi) was decreased (by 14%) under high moisture but increased (by 30%) for drought susceptible cultivars (Kwale, Mbuni and Pasa). Number of tillers/plant was positively correlated to WUE of Duma, Kwale and Pasa but negatively correlated to WUE of Ngamia, Chozi and Mbuni under high moisture situation. However, under low moisture the tillers/plant was positively correlated to the WUE of all the genotypes. Many of the traits studied (tiller/plant, plant height, seeds/spike) had direct positive effect on WUE of drought tolerant cultivars. Although biomass although had a low positive direct effect on WUE but it had a strong indirect positive effect via tillers/plant. This therefore makes biomass a viable indirect selection trait for drought tolerance in wheat genotypes. However, there is need to establish the optimum crop stage at which dependable information would be achieved.

TABLE OF CONTENTS

DECLARATION	i
DEDICATION	ii
ACKNOWLEDGEMENTS	iii
ABSTRACT	iv
TABLE OF CONTENTS	vi
1.0 INTRODUCTION.....	1
1.1 Background information	1
1.2 Hypothesis.....	4
1.3 PROBLEM STATEMENT	4
2.0 LITERATURE REVIEW.....	5
2.1 Introduction	5
2.2 Effect of water stress on yield components	6
2.3 Effect of water stress on root growth.....	8
2.4 Water use efficiency (WUE).....	9
2.5 Correlation and Path effects.....	11
2.6 Morphological traits for selection for drought resistance.....	13
3.0 MATERIALS AND METHODS.....	14
3.1 Experimental site	14
3.2 Description of the rain shelter	14
3.5 Experimental treatments	17
3.6 CULTURAL PRACTICES.....	17
3.7 Measurements	20
3.7.1 Soil water content measurement.....	20
3.7.2 Total water use (ET).....	21
3.7.3 Determination of grain yield and yield components	22
3.7.4 Moisture readings	23
3.8 STATISTICAL ANALYSIS.....	26
4.0 RESULTS.....	27
4.1. Varietal Differences in Grain Yield, Water Use and Water Use Efficiency at High and Low Moisture Levels.....	27
4.2. Varietal differences in growth parameters under two moisture levels	30

4.3. Effects of different agronomic traits on water use efficiency and grain yield of wheat under two moisture levels	33
4.4. Genotypic correlation for agronomic characters affecting grain yield and water use efficiency of wheat under two moisture levels	35
4.4.1. Duma	37
4.4.2. Ngamia	39
4.4.3. Chozi	39
4.4.4. Kwale	39
4.4.5. Mbuni	42
4.4.6. Pasa	42
4.5. Path effects of tiller per plant on water use efficiency of six wheat genotypes	44
4.5.1. Duma	44
4.5.2. Ngamia	44
4.5.3. Chozi	45
4.5.4. Kwale	45
4.5.5. Mbuni	46
4.5.6. Pasa	46
4.6. Path effects of plant height on water use efficiency of six wheat genotypes	49
4.6.1 Duma	49
4.6.2. Ngamia	49
4.6.3. Chozi	50
4.6.4. Kwale	50
4.6.5. Mbuni	51
4.6.6. Pasa	51
4.7. Path effects of biomass on water use efficiency of six wheat genotypes	54
4.7.1. Duma	54
4.7.2. Ngamia	54
4.7.3. Chozi	55
4.7.4. Kwale	55
4.7.5. Mbuni	56
4.7.6. Pasa	56
4.8. Path effects of number of seeds per spike on water use efficiency of six wheat genotypes	58
4.8.1. Duma	58
4.8.2. Ngamia	58
4.8.3. Chozi	59
4.8.4. Kwale	59
4.8.5. Mbuni	60
4.8.6. Pasa	60
4.9. Path effects of tiller number per plant on grain yield of six wheat genotypes	63
4.9.1. Duma	63
4.9.2. Ngamia	63
4.9.3. Chozi	64

4.9.4. Kwale	64
4.9.5. Mbuni	65
4.9.6. Pasa	65
4.10. Path effects of plant height on yield of six wheat genotypes	68
4.10.1. Duma	68
4.10.2. Ngamia	68
4.10.3. Chozi	69
4.10.4. Kwale	69
4.10.5. Mbuni	70
4.10.6. Pasa	70
4.11. Path effects of biomass on yield of six wheat genotypes	73
4.11.1. Duma	73
4.11.2. Ngamia	73
4.11.3. Chozi	74
4.11.4. Kwale	74
4.11.5. Mbuni	75
4.11.6. Pasa	75
4.12. Path effects of seed number per spike on grain yield of six wheat genotypes.....	78
4.12.1. Duma	78
4.12.2. Ngamia	78
4.12.3. Chozi	79
4.12.4. Kwale	79
4.12.5. Mbuni	80
4.12.6. Pasa	80
5.0 DISCUSSION.....	83
5.1. Varietal Differences in Grain Yield, Water Use and Water Use Efficiency at Low and High Moisture Levels	83
5.2. Varietal differences in growth parameters under two moisture levels	86
5.3. Genotypic Correlation for agronomic characters affecting grain yield and water use efficiency (WUE) of wheat under two moisture levels	89
5.4. Path effects on water use efficiency of six wheat genotypes	90
5.4.1. Path effects of tillers/plant on water use efficiency	91
5.4.2. Path effects of plant height on water use efficiency	91
5.4.3. Path effects of biomass on water use efficiency	92
5.4.4. Path effects of seeds per spike on water use efficiency	92
5.5. Path effects on grain yield of six wheat genotypes	93
5.5.1. Path effects of number of tillers per plant on grain yield.....	93
5.5.2. Path effects of plant height on grain yield	94
5.5.3 Path effects of biomass on grain yield	94
5.5.4. Path effects of seeds per spike on grain yield	95

6.0. CONCLUSION AND RECOMMENDATION

95

7.0 REFERENCES

98

LIST OF TABLES

Table 1: Grain yield, water use and water use efficiency of six wheat genotypes under two watering regimes	29
Table 2. Response of the yield components of six wheat genotypes to watering regimes under rainshade at Njoro	32
Table 3. Association of water use efficiency and grain yield with agronomic traits of six wheat cultivars under two moisture regimes	34
Table 4. Pearson correlation coefficients for different agronomic characters (averaged over cultivars) of wheat under high moisture (upper diagonal) and low moisture (lower diagonal) regimes	36
Table 5. Pearson correlation coefficients for Duma under low (below the diagonal) and high (above the diagonal and bold) moisture regime combined	38
Table 6. Pearson correlation coefficients (for Ngamia) under low (below the diagonal) and high (above the diagonal and bold) moisture regime	41
Table 7. Pearson correlation coefficients for Chozi under low (below the diagonal) and high (above the diagonal and bold) moisture levels	41
Table 8. Pearson correlation coefficients (for Kwale) under low (below the diagonal) and high (above the diagonal and bold) moisture regime	41
Table 9. Pearson correlation coefficients (for Mbuni) under low (below the diagonal) and high (above the diagonal and bold) moisture regime	43
Table 10. Pearson correlation coefficients (for Pasa) under low (below the diagonal) and high (above the diagonal and bold) moisture regime	43
Table 11. Direct and indirect path effects of tillers/plant on water use efficiency of six wheat genotypes under two moisture regimes.	48
Table 12. Direct and indirect path effects of plant height on water use efficiency of six wheat genotypes under two moisture regimes.	53
Table 13. Direct and indirect path effects of biomass on water use efficiency of six wheat genotypes under two moisture regimes	57

Table 14. Direct and indirect path effects of seed number per spike on water use efficiency of six wheat genotypes under two moisture regimes	62
Table 15. Direct and indirect path effects of tillers/plant on grain yield of six wheat genotypes under two moisture regimes.	67
Table 16. Direct and indirect path effects of plant height on yield of six wheat genotypes under two moisture regimes.	72
Table 17. Direct and indirect path effects of biomass on the grain yield of six wheat genotypes under two moisture regimes.	77
Table 18. Direct and indirect path effects of seed number per spike on yield of six wheat genotypes under two moisture regimes over seasons	82

LIST OF FIGURES

FIGURE 1: PICTURE OF RAIN OUT SHELTER AT NATIONAL PLANT BREEDING RESEARCH CENTRE	16
FIGURE 2: SOIL MOISTURE CALIBRATION CURVE FOR 0 -20 cm DEPTH.....	24
FIGURE 3: SOIL MOISTURE CALIBRATION CURVE FOR BOTTOM SOIL (30 - 100 cm)	25
FIGURE 4: EXPERIMENTAL FIELD LAYOUT.....	19

1.0 INTRODUCTION

1.1 Background information

Cereals contribute significantly to food security in Kenya (Wanjama *et al.*, 1993). Among cereals, wheat has been ranked second to maize (KARI, 1990) and is grown on an estimated area of 105,000 ha (representing about 6% of the total area under cereal production in Kenya) giving an annual production of about 350,000 metric tonnes (Ekboir, 2002). The crop is mainly grown in the Rift Valley province with Nakuru, Uasin Gishu and Narok districts contributing about 85% of the total national production (Wanjama *et al.*, 1993). The national wheat production has varied over time. For example, in the period 1988 - 2000, wheat production declined annually by about 1.5% (Aquino *et al.*, 2002). The decline in production has been attributed largely to a reduced growth in wheat production area in Kenya.

Due to the reduction in wheat area, Kenya produces only 40% of the national demand of approximately 720,000 tonnes, and importing about 60% of its wheat requirement (Aquino *et al.*, 2002). For example, between 1997-1999, wheat imports stood at 484,900 tonnes (5.4 million 90Kg bags), costing about 5.85 billion Kenya shillings (US\$ 84 million). The slow increase in wheat production relative to increased demand, has resulted in persistent wheat imports since 1990. This has been aggravated by the liberalization of wheat marketing in Kenya resulting in cheap wheat and wheat products being persistently imported (World Bank, 1989). Thus, Kenya is bound to remain a net importer of wheat and wheat products unless domestic wheat production is significantly stepped up. Thus for wheat production to be increased to meet the increasing demand in Kenya, among other technologies, wheat growing has to be expanded to the marginal

rainfall areas which consist of 83% of the total land area with unused arable potential of approximately 200,000 hectares (World Bank, 1989). The relative increase in acreage under wheat production has been greater in the drier wheat growing areas of Kenya (such as Narok district) than in high potential areas (e.g Nakuru district). For example between 1970 and 1992, area under wheat in Narok (low potential) increased by about 81% while a reduction of about 30% (30,782 to 22,472 hectares) was reported in Nakuru district (high potential) (Wanjama *et al.*, 1993). This lop-sided increase in the area under wheat has been attributed to the stiff competition which wheat faces from crops such as maize and other enterprises (e.g livestock) in the high potential areas (Hassan *et al.*, 1992). These areas such as Lower Narok, Laikipia and Kajiado districts are known to be faced with erratic and below average rainfall (<500 mm) during the growing season with high average temperatures of about 32 °C (Jaetzold and Schmidt, 1983).

Furthermore, it has been reported that 32% of the 99 million hectares of wheat grown in developing countries experiences varying levels of drought stress (Rajaram *et al.*, 1996). In Kenya, marginal rainfall areas have been able to achieve wheat yields of between one third and one half of those from high rainfall areas (Kinyua *et al.*, 1989).

Promotion of wheat farming in the dry lands of Kenya can be done through use of irrigation and/or drought resistant wheat varieties. Irrigation would require steady supply of water. Due to scarcity of water in the marginal areas and large initial capital required, irrigation is not easily achievable. Thus development of appropriate varieties for marginal areas may be the most effective alternative for utilizing these areas for crop production. Selection for such varieties requires an understanding of the contribution of the specific

yield components that enhance drought tolerance in wheat genotypes either directly or indirectly. The yield components to be selected for should be those that enhance water use efficiency (WUE) in wheat. This is because drought resistant wheat varieties may be used to maximize on the limited moisture in the marginal environments and breeders can then use the traits in screening wheat lines for drought tolerance. Therefore, the main objective of this study was to evaluate water use efficiency (WUE) as an indirect method for selecting drought tolerant wheat cultivars. The specific objectives were to:

- Assess the differences in WUE of drought tolerant and susceptible wheat genotypes.
- Correlate the agronomic traits associated with WUE among them and evaluate their contributions to grain yield.
- Carry out path coefficient analysis of the traits of wheat genotypes under high and low moisture regimes in order to identify their direct and indirect effects on WUE and grain yield.

1.2 Hypotheses

The two hypotheses that formed the basis of this study were:

- 1). Genetic variation exists in WUE among bread wheat (*T. aestivum* L.) genotypes and agronomic traits are correlated among themselves and to (WUE).
- 2). There are direct and indirect links between agronomic traits and water use efficiency of selected bread wheat genotypes.

1.3 PROBLEM STATEMENT

Wheat was introduced into the highlands of Kenya (mainly Nakuru and Kitale areas) by white settlers at the beginning of twentieth century (Leakey, 1970). Due to stiff competition wheat currently faces from crops such as maize, potatoes and other enterprises such as livestock keeping (Hassan *et al.*, 1992), wheat growing in the recent past has been moved to the non-traditional wheat areas. These new areas of wheat production have resulted into relatively low yields mainly due to drought leading to moisture stress. Drought effects have been detrimental to wheat production because the varieties moved to the drought prone environments were spill-overs and cross-overs from the high potential areas (Maximina *et al.*, 2002).

2.0 LITERATURE REVIEW

2.1 Introduction

On a global scale, drought has been reported as the main environmental factor limiting crop productivity (Fereris, 1987). This limitation of crop productivity is due to the interaction between the frequency of occurrence of water deficits, severity of water stress and stage of the crop at which stress occurs (Wortmann, 1998). For example, some crop growth stages are known to be more sensitive to water stress than others making it difficult to give a precise definition of complete resistance to drought stress (Nyachiro, 1990). Singh (1987) has divided drought stress into different indices which can be exploited in breeding wheat for moisture constrained environments. The indices have been identified as drought avoidance and drought tolerance.

Drought tolerance has been defined differently by various scientists (depending on the mechanism of tolerance). Drought tolerance is the ability of the crop to withstand moisture stress mainly due to increased desiccation tolerance and/or improved turgor or osmo-regulation (Singh 1987; White & Izquierdo 1991). Drought avoidance is thought to be associated with high water conservation and rapid extraction of soil water during moisture stress due to large and deep roots, stomata behaviour, leaf rolling and pubescence (White and Castillo, 1998). In contrast, drought recovery has been defined as the ability of plants to resume growth giving satisfactory yields after moisture stress (Wortmann, 1998). This mechanism may be associated with shallow roots which enhance rapid water uptake as soon as moisture is replenished in the soil and/or hypersensitivity where tissues enter dormancy but resume growth immediately moisture situation improves. Such mechanisms have been reported to utilize water that would otherwise be

lost from direct evaporation. Wheat cultivars developed for water stressed environments should thus have the mechanism(s) for drought tolerance, resistance or escape. Therefore, breeders working in environments where water stress is the most important factor limiting crop production need to develop simple and fast methods to select drought resistant cultivars (Cedola *et al.*, 1994).

2.2 Effect of water stress on yield components

The use of yield and yield components in selecting for drought tolerance in small cereals was earlier proposed by Engledow and Waddan (1923) and has lately been supported by Kinyua *et al.*(1993). A number of studies have shown that yield of small grain cereals could be improved by selecting for several yield components such as thousand kernel weight (TKW) and harvesting index (HI) (Ayiecho and Onim 1983; Adams 1987; Woodworth 1989; and Agwanda *et al.*, 1989).

Many yield components influence grain yield in wheat under field conditions. Such yield components include spikes density, number of spikelets/spike and the number of grains/spike. Crop varieties adapted to dry areas must integrate a number of characteristics that enhance their efficient use of moisture (Mather and Jinks, 1971). However, the effect of those traits can be counteracted by small number of grains per spike and low kernel weight resulting in low yields under drought (Hampton *et al.*, 1981; Lewis *et al.*, 1997). Grain yield of wheat has been shown to be linearly correlated to spike number and grains per unit area or per spike (Bullman and Hunt, 1986). Although

the number of grains per spike and kernel weight have been reported to compensate somewhat for different spike densities, they may not adequately make up account for the yield potential (Nelson, 1980).

Yield components have been reported to behave differently under drought. For example, Kheiralla (1994) reported a reduction in spike length (by about 12%), 1000-kernel weight (by about 9%) and grain yield (by about 40%) on six spring wheat genotypes under drought. However, some genotypes and their hybrids were relatively more tolerant than others. Also, the duration of water stress has been reported to affect yield components differently. One study has shown that as water stress increased, grain number was reduced but kernel weight remained relatively insensitive (El Hafid *et al.*, 1998).

Furthermore, the stage at which drought stress appears has also been reported to have varying effects on yield components. In a study by Volke and Fernandez (1973), wheat exposed to drought at tillering stage resulted in decreased 1000-kernel weight, grain yield, number of spike-lets/spike. However, the number of kernels per spike was not adversely affected after exposing wheat to reduced moisture for five days. Wheat at anthesis exposed to longer periods of drought stress resulted in decreased grain yield, the number of spikes per plant and also in the number of kernels/spike whereas 1000-grain weight was increased. However, grain number/spike and number of spikes/m² were highest under non-stressed conditions. Consequently an increase in the number of spikes/m² resulted in more grains per spike and low grain weight (Simane *et al.*, 1993).

2.3 Effect of water stress on root growth

Drought affects the overall development of the crop through its organs. The level of sensitivity to drought also depends on the part of crop affected. For example, in a study conducted by Petr *et al.* (1988), water was reported to be one of the most important factors affecting underground plant organs. In that regard, roots were reported to be more affected by excess or deficit of soil moisture than above-ground parts. In the same study, it was realized that roots of wheat usually extend to greater depths in dry regions than in moist environments.

Wheat cultivars developed for dry environments extend their roots depending on the depth at which moisture is concentrated in the soil profile. In a study by Stoppler *et al.* (1991), improved drought resistance of modern wheat varieties was found to be associated with extensive and deep rooting. Extensive and deep roots at the start of grain filling appeared to be necessary to achieve high ear weight under drought situation. In other studies several wheat crop parameters have been reported to respond differently to varying soil moisture situations. For example, Bharti *et al.* (1990) observed better root growth with irrigation, and maximum root density at 10-20 cm depth for all varieties tested. In contrast, Narayan (1991) observed increased root density in the soil profile under high moisture situation and deeper root penetration under moisture stress. Under moisture stress conditions, cultivars with deeper roots have been observed to yield higher than the ones with shallower roots. Thus under soil moisture stress environment the root penetration depth was a better criterion than total root length density for selecting suitable cultivars of wheat for a higher yield (Narayan, 1991).

Ratio of root to shoot dry matter has been used as a criterion for drought tolerance. In a study by Wahbi and Gregory (1990) varieties of wheat with a high ratio of root to shoot dry matter (DM) showed greater nutrient uptake, yield stability and drought resistance. A close relationship between root volume, root weight and grain yield was also noted in a moisture stressed environment such that varieties that had higher root volume and weight gave higher yields (Bangal *et al.*, 1988). Competition between roots and the wheat ears for carbon has been observed to vary with moisture regimes. The pattern of carbon allocation between respiration and carbon accumulation changed in roots soon after imposition of drought. Although total root respiration decreased under drought it became more energy efficient and this was due to the fact that less respiration took place via the alternative pathway.

2.4 Water use efficiency (WUE)

Water availability often limits crop production in rain-fed agriculture. Rain-fed crop production in regions with low and variable rainfall may be maximized by ensuring water is extracted thoroughly from the soil profile and/or efficiently used by the crop plants (Ogola, 1999). Therefore, the development of wheat cultivars that use available moisture more efficiently and that are able to tolerate drought is a major goal for increasing productivity in drought prone environments. Water use efficiency (WUE) is considered an important component of adaptation to drought.

Genetic variation for plant WUE exists both among and within species (Briggs and Shantz, 1914). Water use efficiency in plants has been defined as the ratio of total dry matter per unit water used (Begg and Turner, 1976; Ogola, 1999). In most crops species, only a portion of the total biomass is of economic importance, and WUE is therefore defined as harvested yield per unit of water consumed (Evans and Wardlaw, 1976). Water use efficiency has also been defined at the leaf level as the ratio of photosynthesis (net CO₂ assimilation) per unit water transpired (Fischer and Turner, 1978; Sinclair *et al.*, 1984; Gregory, 1989). However, for the purpose of this study, the working definition of WUE will be as stated by Evans and Wardlaw (1976).

Water use efficiency has been reported to have a highly significant relationship with yield in wheat (Olson *et al.*, 1964; Musick *et al.*, 1994) and other crops (Power, 1985;). Such relationships may either be positive or negative depending on the moisture status.

Genotypes to be grown in marginal areas should maximize water use efficiency (WUE) by increasing transpiration efficiency (TE: ratio of total above ground dry matter produced (DM) to total amount of water used by the crop, T) and also increasing amount of water transpired relative to bare surface evaporation (Esc). However, for any given crop and environment, TE varies little (Sinclair *et al.*, 1984) therefore increasing WUE lies in the ability to extract water more thoroughly from the soil and/or reducing Esc. Thus genotypes that are able to maximize WUE by increasing TE and decreasing Esc should be a candidate for selection for marginal areas. From this review the mechanisms of resistance to drought tolerance was used to explain the results of the study.

2.5 Correlation and Path effects

Path effect analysis was first proposed by Wright (1921) and elaborated by Dewey and Lu (1959). The technique has been used to determine the relationship between correlated characters in spring wheat (Walton 1972) and elaborately in population genetics in wheat (Li, 1976). In some qualitative studies, Costa and Kronstad (1994) used path analysis to study the relationship between wheat grain protein concentration as affected by grain yield and biological yield, harvest index and related traits in the Pacific Northwest environment at Oregon in the USA.

The technique has also been used to evaluate the contribution of yield components in water use efficiency (WUE) in wheat. The contribution of each yield component trait to variation in WUE in wheat was evaluated using path coefficient analysis technique (Ehdaie and Waines, 1993). Simane *et al.*(1993) revealed a complex pattern of relationships among 6 variables in wheat yield components by use of path analysis technique. Also Kinyua (1991) used path analysis technique to evaluate the effect of yield components on yield and found that tillers per plant, plant height, spikelets per head, seeds per head and kernel weight had high direct effect on grain yield. Characterization of major yield components of spring wheat on sensitivity to Canadian thistle competition (following field trials at Fargo) was also done using path coefficient analysis technique (Donald and Mohammad, 1996). Camacho *et al*, (1995) while studying the relationships among heading date, plant height, disease severity, and grain yield in wheat cross, used phenotypic correlations and path coefficient analyses.

Path analysis technique has also been used in other cereals. For example, in maize correlation and path coefficient analyses have been used to evaluate the impact of stalk water on stalk lodging resistance and grain yield (Djordjevic and Ivanovic, 1996). Path coefficient analysis technique has also been used in the evaluation of the associations among seed yield components under different defoliation treatments in pearl millet x elephant grass hybrids (Diz *et al.*, 1995). The technique was used to evaluate the effects of 11 panicle characters on grain yield of twenty high yielding rice genotypes (Ramalingam *et al.*, 1993).

A part from cereals, the technique has also been used on other crops. For example, path coefficient analysis has been used to study the effects of leaf and stem growth rates on length of the vegetative period and N concentration in Flax (Dybing and Grady, 1994). Evaluation of direct and indirect effects of components of seed yield and those of leaf number and leaf size upon components of seed yield in bambara groundnut germplasm from Ghana (Ofori, 1996). Relationships between tuber yield and yield components (as influenced by cultivar and N fertilizer application) in potatoes was studied using path coefficient analysis based on an ontogenetic model (Morena *et al.*, 1994). Field resistance of field crops to diseases has also been studied using path effects. For example, genetic parameters of the components of field resistance of potatoes to late blight (*Phytophthora infestans*) using detached leaves from 16 potato cultivars were studied using path analysis (Birham and Singh, 1995). Path coefficient analysis has also been used in palm trees to study the relationship between the effect of number of bunches per palm on oil yield, bunch weight and percentage oil-to-mesocarp ratio in palm oil (Ataga, 1995). Further, it

was also used in a study involving improvement of yields in rapeseed (*Brassica campestris*, *B.napus*) (Thurling, 1974).

2.6 Morphological traits for selection for drought resistance

Different morphological traits have been associated with different functions under different moisture regimes. The morphological traits that have been identified to associate with drought resistance in wheat include seed size, coleoptile length, early ground cover, pre-anthesis biomass and thickness, high tiller survival and stay green (Reynolds *et al.*, 1999). Siddique *et al* (1990) reported that improved mechanisms of partition between straw and grain yield (improved HI) were the main causes of increased grain yield (under moisture stress) in drought prone (e.g Mediterranean-type) environment. Simane *et al* (1993) and El Hafid *et al.*(1998) reported that drought resistant durum wheat cultivars had rapid early ground cover, maintained high green leaf area and higher reproductive tiller survival. Similarly, wheat breeding at CIMMYT has documented stay green, leaf rolling and firing as positive traits for increasing yield under stress (Richards *et al.*, 2001). If such traits could be in a wheat variety identified then they may be used as indirect selection criteria more easily and efficiently in wheat breeding program for drought tolerance.

3.0 MATERIALS AND METHODS

3.1 Experimental site

An experiment was conducted in the rain shelter for two seasons between August, 2001 and May, 2002 at the National Plant Breeding Research Centre (NPBRC), Kenya ($0^{\circ} 20'$ S and $35^{\circ}56'E$ and altitude 2185 metres) [NPBRC Meteorological Station No. 9035021, 1999].

The site lies within the Agro-ecological zone LH3 (AEZ LH3) with a bimodal rainfall pattern (Jaetzold and Schmidt, 1983). The site receives an annual rainfall of about 960 mm with an average maximum and minimum temperatures of $24^{\circ} C$ and $8^{\circ} C$, respectively (NPBRC, Njoro Meteorological station No.9035021, 1999).

The soil at the site is well drained, deep to very deep, dark reddish brown, friable and smearable, silt clay, with humic topsoil classified as mollic Andosols (Jaetzold and Schmidt, 1983). The site was under fallow for two seasons before this study was carried out.

3.2 Description of the rain shelter

The experiment was carried out under a mobile rain-out shelter (which is an open ended structure measuring 30 m long and 7 m wide) to exclude rain and consequently induce drought stress (Fig.1). The shelter consists of a roof mounted on wheels that allows it to roll on two parallel-elevated concrete tracks. Translucent sheets (which allow up to 90% photosynthetic photon flux density) covered the roof. The sides had metal frames, which were covered by foldable polythene sheets, with open-end 0.5 m above the ground. A concrete barrier had also been constructed to a depth of 0.6 m below the ground level and 0.15 m above the ground level along the two longer sides of the shade from a rail. The

length of the rail was 30 m but the shelter rested on half the length. The barrier also helped to prevent the rainwater from flooding the shade (Figure 1) (Legg *et al.* (1978) and Upchurch *et al.* 1983).

FIGURE 1: RAIN OUT SHELTER AT THE NATIONAL PLANT BREEDING RESEARCH CENTRE



3.5 Experimental treatments.

Six bread wheat genotypes Duma, Chozi, Ngamia, Kwale, Mbuni and Pasa were grown under two watering regimes (High and low watering regimes) for two seasons. The experiment was replicated three times and laid out in a randomized complete block design (RCBD) with split plot arrangement with the watering regime being the main plot and cultivar as sub-plot (Figure 4).

Thirty-six (36) PVC access tubes (39.4 mm and 41.4 mm as internal and outside diameters, respectively) were installed in the field before planting. In each sub-plot, an access tube was installed in holes drilled by hand using a soil auger. The tubes were cut to a depth of 1.7 m out of which 1.1 m was driven into the holes and 0.6 m was left above the soil surface. Moisture readings were taken by use of a Troxler moisture meter (Neutron probe).

3.6 CULTURAL PRACTICES

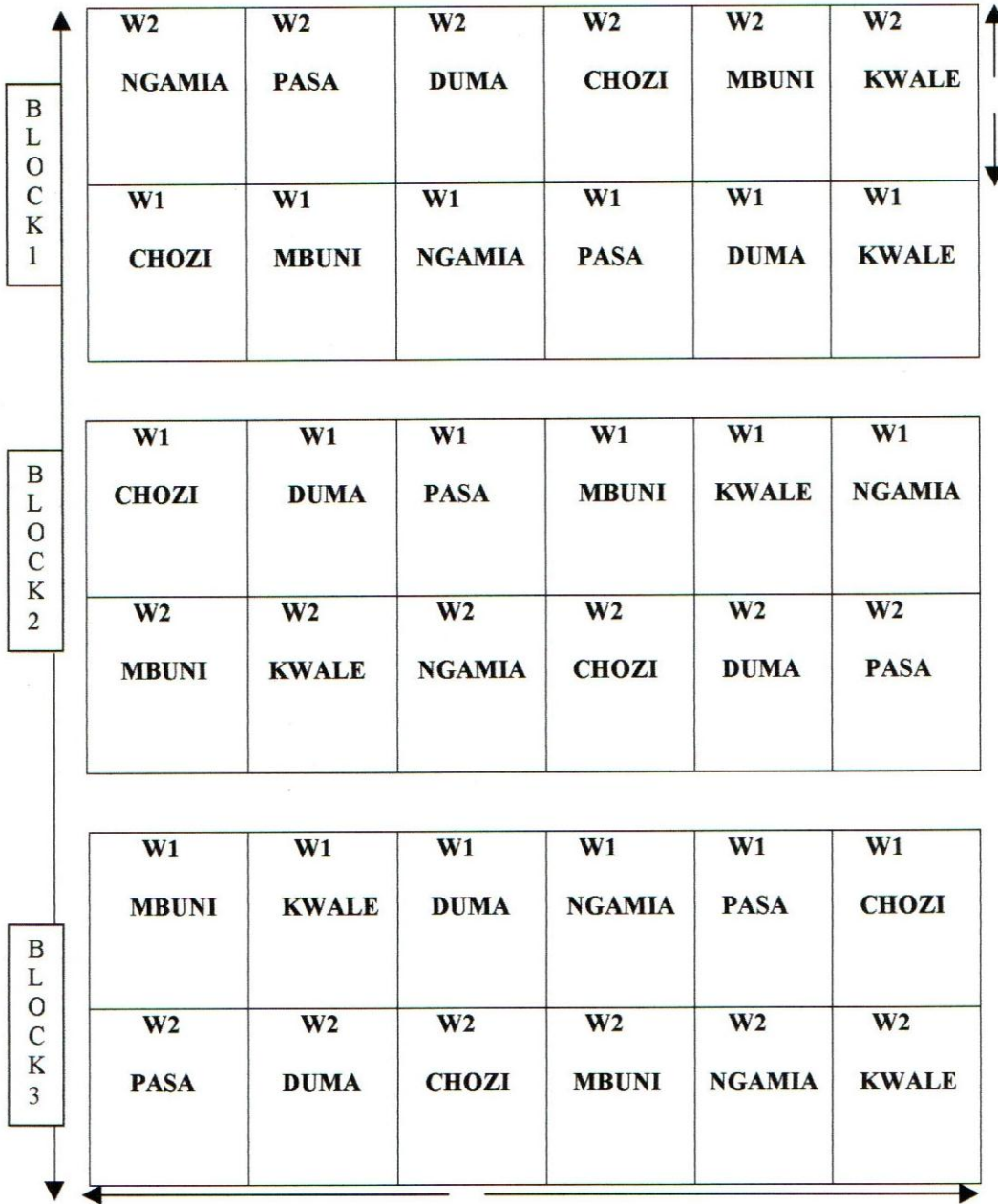
The seeds of the wheat varieties used in the trial were tested for germination before planting and the seed-rate was adjusted according to the germination percentage. The recommended seed-rate of 125 kg ha⁻¹ was used.

The six cultivars were planted in plots of 0.8 metres length and 2 metres width with ten rows. The rows were 20 cm apart and planting was done by hand. The seeds were drilled continuously on the furrows (5 cm deep) made by hand. Triple super-phosphate (0-46-0) was applied in the furrows at 60 kg P₂O₅ ha⁻¹ at planting and calcium ammonium nitrate (CAN) at 40 kg N ha⁻¹ (recommended rate) was top-dressed at early

tillering stage. Water was supplied through drip irrigation at a constant pressure as per the treatments. One drip lateral was laid between two wheat rows.

Watering was done weekly and a day before watering was done moisture reading were taken by use of neutron probe. Watering was done when the moisture level had come to 50% field capacity. The high moisture treatment received 14.5 mm and the low moisture regime received 7.5 mm weekly. The total amount of water applied during each season was 217 mm and 113 mm for the high and low moisture regimes, respectively.

Weed control was done by the use of Buctril Mc at the rate of 1.4 L ha⁻¹ at the 3-4-leaf stage of crop. The chemical was used to take care of broad-leaved weeds but for the grasses, hand weeding was done.



KEY: W1 & W2 = High and low watering regimes, respectively

Figure 4: Experimental field layout

3.7 Measurements

The following parameters were measured:

- Soil water content
- * Total crop water use/Evapotranspiration (ET)
- * Total dry matter (TDM)
- * Grain yield (GY)
- * Harvest index (HI).
- * Thousand kernel weight (TKW)

3.7.1 Soil water content measurement

The soil profile of the site (NPBRC field 1) was described and the soil depth of the site determined and the pumice was realized to start immediately after 60-cm depth. For calibration, two access tubes were installed each at a depth of 110 cm. One of the tubes was used to get wettest point of the calibration curve whereas the other one was for the drier points of the curve (Ooro *et al.*, 2001).

The place surrounding the tube for the wettest point was flooded with water and left to settle for 24 hours and then soil samples for gravimetric moisture determination were taken at 10, 20, 30, 40, 60, 80 and 100 cm depths. At the corresponding depths, neutron probe readings were taken for the hydrogen ion counts and hence volumetric water content. The same approach was used around the access tube for the lower points of the calibration curve (Manual of Operation and Instruction, 1996).

The data generated from the neutron probe readings (from the wet and dry calibration spots) were used to calculate count ratios (H^+ /Standard count) plotted on the x-axis of the calibration curves (Figures 2 and 3) and two equations were then developed for the top soil (upper 20 cm) and below 20 cm depths, respectively. The two calibrations were developed due to the variations between the readings of depths up to 20 cm and those below 20 cm. Hydrogen ions readings up to 20 cm depth were relatively lower due to scatter effect while this effect did affect readings below 20 cm. The equations were developed by plotting gravimetric moisture readings on the y-axis and the count ratios on the x-axis. The equations were as follows:

$$0 - 20 \text{ cm depth: } Y = 0.0661n + 0.001615 \quad (3.1)$$

$$30 - 100 \text{ cm depth: } Y = 0.20960n + 0.001132 \quad (3.2)$$

Whereas Y is the actual moisture (volumetric moisture)

n = count ratios (H^+ /standard counts) [H^+ was read from the neutron probe]

3.7.2 Total water use/Evapotranspiration (ET)

Evapo-transpiration (ET) included both transpiration and direct evaporation of water from the soil surface (E_{sc}). Evapo-transpiration was determined by using the soil water balance equation given below:

$$ET = -\Delta S + I - D - R \quad (3.4)$$

Where $-\Delta S$ is the change in storage (obtained by the difference in volumetric moisture content of the entire profile at the beginning and end of the season), I is irrigation water applied, D is the drainage and R is the run-off. Drainage and run-off were assumed to be negligible hence total crop water use for the whole season obtained by summing total

irrigation and changes in storage for the entire profile (Ogola, 1999). Pilbeam *et al.*, (1995) suggested that significant drainage is considered to have occurred where the soil water at the base of the profile was increased above its initial value. Drip irrigation was used hence runoff was assumed to be zero and thus not included in the water balance equation.

3.7.3 Determination of grain yield and yield components

Grain yield (GY) was determined by harvesting one metre length of the two inner-most rows. Six innermost rows were hand harvested for biomass and grain yield determination.

Harvesting was done by hand. The harvested material was threshed by the use of laboratory single head thresher and grain yield was standardized at 12.5% moisture content.

Thousand-kernel weight (TKW) was determined after grain weight had been recorded from both experiments. A thousand seeds were picked randomly and weighed to determine TKW.

Harvest index (HI) was determined from grain yield (GY) and dry matter (DM) as follows:

$$HI = GY/DM. \quad (3.5)$$

3.7.4 Moisture readings

Moisture readings were taken by use a Troxler moisture meter (Neutron probe). In the process of moisture reading a standard count was at the beginning of each moisture regime.

Hydrogen ions, standard counts and moisture percentage by volume readings were taken through the access tubes at an interval of 7 days at an interval of 10 cm in the upper 40 cm and 20 cm below 40 cm. The hydrogen counts were divided by the standard counts to derive the count ratio that was later fitted in the calibration equations, for different soil levels within the profile, to calculate the actual soil water content.

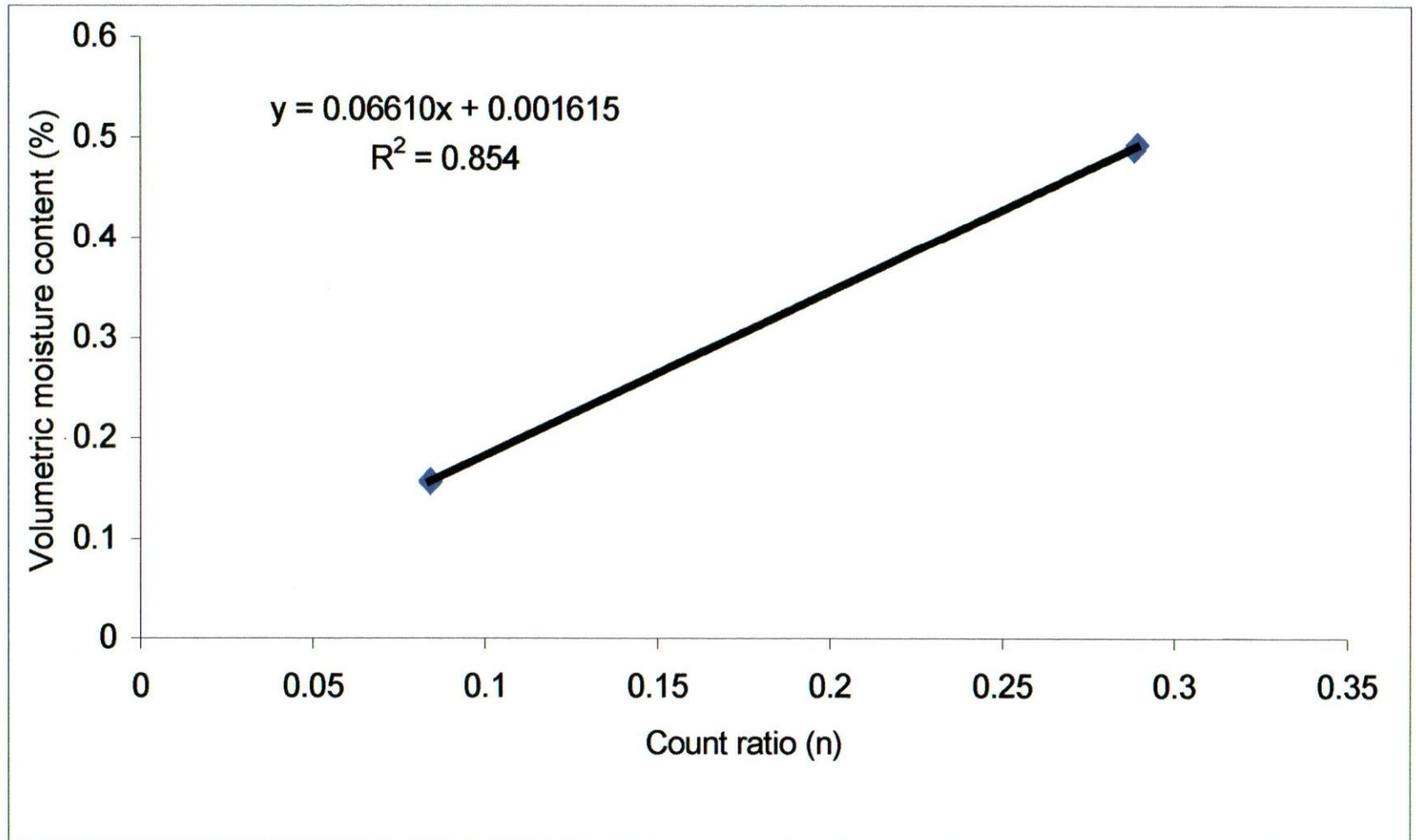


Figure 2: Soil Moisture Calibration curve for 0 – 20 cm soil depth

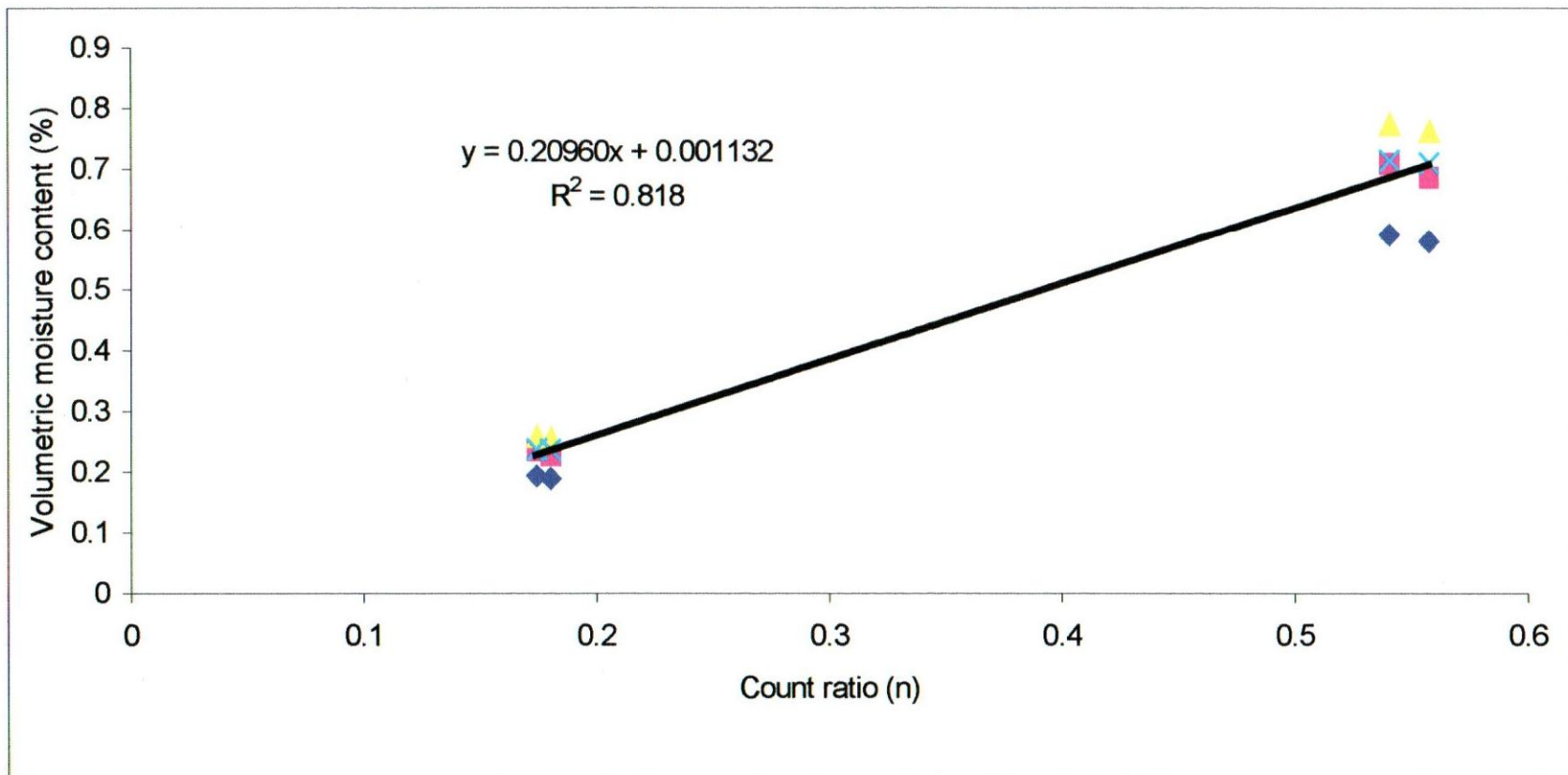


Figure 3: Soil Moisture Calibration curve for bottom soil (30 – 100 cm)

3.8 STATISTICAL ANALYSIS

Data from all the parameters, combined over two seasons (2001 and 2002), were subjected to an analysis of variance (ANOVA) using SAS (SAS User's guide, 1985). Least significant difference procedure (LSD) was used to carry out mean separations. The data was also subjected to correlation and path coefficient analysis was done to separate the direct and indirect effects between the agronomic traits and water use efficiency (Ataga 1995).

4.0 RESULTS

4.1. Varietal Differences in Grain Yield, Water Use and Water Use Efficiency at High and Low Moisture Levels

The interaction between genotype and moisture regime affected final grain yield. High watering regime increased grain yield of both the drought tolerant and drought susceptible varieties but the increase in yield due to high watering regime was greater in susceptible (110%-134%) than in tolerant (55-64%) varieties (Table 1). The drought tolerant varieties produced greater yield than the drought susceptible ones under low watering regime. Under high moisture regime, in contrast, the drought sensitive varieties produced greater yields than the tolerant ones.

There was significant effect of the interaction between moisture regime and cultivar on crop water use, such that the increase in water use due to high watering regime was greater for drought sensitive (96%) than for drought tolerant (93%) varieties. Also, under low moisture conditions Kwale used more water (by 10%) than all the other cultivars tested while under high moisture, Chozi had significantly lower (by 3%) water use value than the rest of the cultivars (Table 1). Significant genotypic differences on water use were detected. Averaged over the watering regimes, Kwale had the highest water use (139 mm) while Pasa had the lowest water use (132 mm) (Table 1). High watering regime increased water use (averaged over all varieties) by 95% (from 91 to 177 mm) (Table 1).

The interaction between variety and moisture regime affected water use efficiency (WUE) (Table 1). High moisture regime decreased (by 10%-19%) WUE of drought

tolerant varieties (Duma, Ngamia and Chozi) but increased (by 26%-29%) WUE of drought sensitive varieties (Kwale, Mbuni and Pasa). Under low moisture regime, drought tolerant varieties had higher WUE values than the drought sensitive varieties while the converse was true under high moisture level (Table 1). No significant effects of cultivar on WUE were detected. However, high watering regime increased WUE (averaged over all wheat varieties) by 4% (from 9.6 to 9.9 kg ha⁻¹ mm⁻¹) (Table 1).

Table 1. Grain yield, water use and water use efficiency of six wheat genotypes under two watering regimes under rainshade at Njoro

Treatment		Grain Yield (kg ha ⁻¹)	Water Use (mm)	Water Use Efficiency (kg ha ⁻¹ mm ⁻¹)
Moisture regime	Cultivar			
Low				
	Duma	1213.0ab	90.0b	10.7ab
	Ngamia	1286.0a	91.0b	10.9a
	Chozi	1324.0a	91.0b	11.1a
	Kwale	1152.0abc	98.0a	9.0b
	Mbuni	902.0bc	88.0b	7.9c
	Pasa	862.0c	87.0b	7.7c
High				
	Duma	1886.0b	177.0a	8.7b
	Ngamia	2097.0b	177.0a	9.8ab
	Chozi	2173.0ab	171.0b	9.6b
	Kwale	2424.0a	179.0a	11.3a
	Mbuni	2114.0ab	177.0a	10.1ab
	Pasa	2020.0b	177.0a	9.9ab
SE		10.99	2.96	0.58
F-test probabilities				
Irrigation (I)		P<0.01	P<0.01	P<0.05
Cultivar (C)		P<0.05	P<0.05	ns
Interaction (CXI)		P<0.05	P<0.01	P<0.01

Figures followed by the same letter within the same moisture regime in the same column are not significantly different at LSD 5%.

4.2. Varietal differences in growth parameters under two moisture levels

There was a significant interaction between moisture regime and cultivar on the number of tillers per plant. High watering regime increased (by 34%-54%) number of tillers per plant of Kwale, Ngamia and Chozi but decreased (by 16%-21%) number of tillers per plant of Duma, Mbuni and Pasa (Table 2). Also, the number of tillers per plant varied with cultivar, ranging from 3.2 (Ngamia) to 5.1 (Pasa) (Table 2). High moisture regime increased (by 8%) number of tillers per plant (Table 2).

The interaction between moisture regime and wheat cultivar affected plant height (Table 2). High watering regime increased the plant height of drought tolerant varieties to a greater (by 27%-40%) extent than those of drought sensitive varieties (12%-33%). Under low moisture Chozi and Pasa were the tallest cultivars while Ngamia was the shortest. In contrast, under high moisture regime, Chozi and Pasa were the tallest and shortest cultivars, respectively (Table 2). On average, drought tolerant varieties were taller (by 4%) than drought susceptible ones under high moisture regime but the drought susceptible ones were taller (by 4%) under low moisture regime (Table 2). No significant differences on plant height due to cultivar were detected (Table 2). High watering regime increased plant height (averaged over all cultivars) by 29% (Table 2).

Differences between varieties on TKW varied with moisture regime. On average, drought tolerant varieties (Duma, Ngamia, Chozi) gave higher TKW under high moisture than drought susceptible (Kwale, Mbuni, Pasa) varieties. In contrast, under low moisture, drought sensitive varieties gave higher TKW than the tolerant ones (Table 2). Genotypic

differences on TKW were significant (Table 2). When averaged over the two watering regimes, Chozi had the highest (48) TKW while Ngamia had the lowest (40). No significant effects of moisture regime on TKW were detected (Table 2).

There was a significant interaction between watering regime and wheat cultivar on seed number per spike (Table 2). High moisture regime increased seed number per spike of Duma (by 21%), Chozi (by 4%), Kwale (by 36%), and Pasa (by 19%); had no effect on seed number per spike of Mbuni; and decreased (by 10%) seed number per spike of Ngamia. Also, the increase in seed number per spike due to high moisture regime was higher for the drought sensitive (19%-36%) than the drought tolerant (4%-21%) varieties. The effect of cultivar on seed number per spike was significant (Table 2). Averaged over the two watering regimes, Pasa had the highest (40) while Chozi had the lowest (28) seed number per spike. On average, drought susceptible varieties (Kwale, Mbuni, Pasa) recorded higher seed number per spike (35) than drought tolerant (Duma, Ngamia, Chozi) varieties (32). High moisture regime increased seed number per spike (averaged over cultivars) by 9% (Table 2).

Table 2. Response of the yield components of six wheat genotypes to two watering regimes under rainshade at Njoro.

Treatment		No. of tillers/plant	Plant height (cm)	TKW (g/1000 seeds)	No. of seeds/spike
Moisture regime	Cultivar				
Low					
	Duma	4.5ab	53.0b	43.0b	26.0c
	Ngamia	2.7c	52.0b	39.0c	40.0a
	Chози	3.7bc	58.0a	46.0a	27.0bc
	Kwale	3.5bc	55.0ab	45.0ab	25.0c
	Mbuni	4.0b	55.0ab	46.0a	35.0abc
	Pasa	5.7a	58.0a	43.0b	36.0ab
High					
	Duma	3.8bc	69.0bcd	44.0bc	33.0b
	Ngamia	3.7bc	66.0cd	41.0d	36.0ab
	Chози	5.7a	81.0a	49.0a	28.0b
	Kwale	4.7ab	70.0bc	46.0b	34.0ab
	Mbuni	3.3c	73.0bc	42.0cd	35.0ab
	Pasa	4.5abc	65.0d	40.0d	43.0a
SE		0.63	2.49	1.46	8.95
F-test probabilities					
Irrigation (I)		P<0.01	P<0.05	ns	P<0.01
Cultivar (C)		P<0.01	ns	P<0.05	P<0.05
Interaction (CXI)		P<0.05	P<0.01	P<0.01	P<0.01

Figures followed by the same letter within the same moisture regime in the same column are not significantly different at Lsd 5%.

4.3. Effects of different agronomic traits on water use efficiency and grain yield of wheat under two moisture levels

Results of the analysis of the effects of different agronomic traits (number of tillers per plant, plant height, biomass, TKW, seed number per spike and harvest index) on water use efficiency and grain yield of the six wheat genotypes under two moisture regimes are presented in Table 3. Biomass had a significant ($P < 0.01$) positive effect on WUE under both low and high moisture regimes. Also, biomass and HI had a significant ($P < 0.01$) positive effect on grain yield under both low and high moisture conditions. In contrast, TKW had a significant ($P < 0.05$) negative effect on grain yield under low moisture regime.

Table 3. Association of water use efficiency and grain yield with agronomic traits of six wheat cultivars under two moisture regimes

Moisture regime	Correlation coefficient	
	Water use efficiency	Grain yield
Low moisture		
Number of tillers/plant	0.031	0.889
Plant height	-0.235	-0.052
Biomass	4.704**	3.348**
TKW	0.898	-1.921*
Seed number/spike	-1.082	-1.506
HI	-1.032	7.082**
High moisture		
Number of tillers/plant	1.273	-1.014
Plant height	-1.833	-0.159
Biomass	13.302**	4.275**
TKW	1.167	-0.301
Seed number/spike	0.127	-1.216
HI	1.491	7.938**

* significant at $P < 0.05$

** significant at $P < 0.01$

4.4. Genotypic correlation for agronomic characters affecting grain yield and water use efficiency of wheat under two moisture levels

Several agronomic traits (number of tillers per plant, plant height, biomass, TKW, seed number per spike and harvest index) of six wheat genotypes were correlated with each other and their effects on grain yield and WUE are presented in Table 4. Biomass and HI showed significant ($P < 0.01$) correlation ($r = 0.439$ and $r = -0.560$, respectively) with water use efficiency under low moisture. Under high moisture, seed number per spike ($r = -0.677$) and plant height ($r = -0.503$) showed significant ($P < 0.01$) negative correlation with WUE (Table 4).

Grain yield was positively correlated to most of the traits studied under both moisture regimes. Under low moisture HI ($r = 0.972$), biomass ($r = 0.928$), plant height ($r = 0.838$), seed number per spike ($r = 0.797$) and TKW ($r = 0.313$) showed significant positive correlation with grain yield while WUE ($r = -0.437$) showed a significant negative correlation with yield (Table 4). Under high moisture, HI ($r = 0.961$), plant height ($r = 0.848$), seed number per spike ($r = 0.816$), biomass ($r = 0.809$), and TKW ($r = 0.514$) showed significant ($P < 0.01$) positive correlation with grain yield (Table 4).

Table 4. Pearson correlation coefficients for different agronomic characters (averaged over cultivars) of wheat under high moisture (upper diagonal) and low moisture (lower diagonal) regimes

	Tillers	Height	Biomass	TKW	Seed/spk	HI	WUE	Yield
Tillers	-	0.163	-0.036	0.249	-0.035	0.053	-0.039	0.008
Height	0.075	-	0.622**	0.412*	0.711**	0.863**	-0.503**	0.848**
Biomass	0.023	0.827**	-	0.438**	0.476**	0.682**	0.102	0.809**
TKW	0.066	0.705**	0.573**	-	0.146	0.262	0.106	0.514**
Seed/spk	-0.034	0.870**	0.736**	0.484**	-	0.857**	-0.677**	0.816**
HI	-0.061	0.879**	0.866**	0.568**	0.892**	-	0.066	0.961**
WUE	0.073	0.056	0.439**	0.161	-0.105	-0.560**	-	0.211
Yield	-0.015	0.838**	0.928**	0.313*	0.797**	0.972**	-0.437**	-

* significant at $P < 0.05$

** significant at $P < 0.01$

The correlation analysis was further carried out for each of the six wheat cultivars (Duma, Ngamia, Chozi, Kwale, Mbuni and Pasa) and the results for each variety are discussed separately.

4.4.1. Duma

Tiller number per plant ($r = 0.953$) showed a significant ($P < 0.01$) positive correlation with WUE under low moisture while under high moisture tiller number per plant ($r = -0.836^*$) was negatively correlated ($P < 0.05$) to WUE (Table 5).

Biomass ($r = 0.983$), WUE ($r = 0.974$), plant height ($r = 0.918$), seed number per spike ($r = 0.837$), tiller number per plant ($r = 0.817$), HI ($r = 0.789$) and TKW ($r = 0.779$) had significant positive correlation with yield under low moisture regime (Table 5). Under high moisture in contrast, it is only HI ($r = 0.946$), plant height ($r = 0.916$) and TKW ($r = 0.822$) that showed significant positive correlation with grain yield (Table 5).

Tiller number per plant was positively correlated to both WUE ($r = 0.953$) and yield ($r = 0.817^*$) under low moisture but not under high moisture. However, under high moisture regime, tiller number per plant was negatively correlated to WUE ($r = -0.836$).

Table 5. Pearson correlation coefficients for Duma under low (below the diagonal) and high (above the diagonal and bold) moisture regime combined

	Tillers	Height	Biomass	TKW	Seed/spk	HI	WUE	YIELD
Tillers	-	0.553	-0.276	0.362	0.837*	0.518	-0.836*	0.283
Height	0.549	-	0.403	0.652	0.827*	0.985**	-0.514	0.916*
Biomass	0.714	0.944**	-	0.743	0.234	0.451	0.442	0.709
TKW	0.347	0.909*	0.861*	-	0.725	0.723	-0.201	0.822*
Seed/spk	0.373	0.945**	0.907*	0.908*	-	0.828*	-0.625	0.704
HI	0.693	0.974**	0.973**	0.845*	0.912*	-	-0.522	0.946**
WUE	0.953**	0.485	0.696	0.399	0.335	0.619	-	-0.259
YIELD	0.817*	0.918**	0.983**	0.779*	0.837*	0.789*	0.974**	-

* significant at $P < 0.05$

** Significant at $P < 0.001$

4.4.2. Ngamia

None of the agronomic traits studied showed significant correlation with WUE under both watering levels (Table 6). There was a high positive effect of HI ($r = 0.994$), plant height ($r = 0.943$), biomass ($r = 0.972$), seed number per spike ($r = 0.964$) and TKW ($r = 0.807$) on grain yield under low moisture level (Table 6). Under high moisture, HI ($r = 0.965$) and plant height ($r = 0.961$) showed a strong positive correlation with grain yield (Table 6). Moreover, HI ($r = 0.985$) and TKW ($r = 0.908$) were positively correlated to Biomass while HI ($r = 0.945$) was positively correlated to seed number per spike under low moisture (Table 6).

4.4.3. Chozi

The agronomic traits studied (number of tillers per plant, plant height, biomass, TKW, seed number per spike and harvest index) did not show significant correlation with WUE under low moisture regime (Table 7). Under high moisture, however, seed number per spike ($r = -0.907$), HI ($r = -0.897$), plant height ($r = -0.824$) and biomass ($r = -0.823$) were negatively correlated with WUE (Table 7). Plant height, number of seeds per spike, biomass and HI showed positive significant correlation with yield of Chozi under both moisture regimes. Also, TKW ($r = 0.913$) correlated positively with grain yield under low moisture while WUE ($r = -0.886$) correlated negatively with yield under high moisture (Table 7).

4.4.4. Kwale

The correlation between different yield components and WUE of Kwale was not significant under low moisture. However, seed number per spike ($r = -0.812$) showed a

significant negative correlation with WUE under high moisture (Table 8). There was a significant positive correlation between seed number per spike, plant height, biomass and HI, and grain yield under both moisture levels while TKW was positively correlated to yield only under low moisture regime (Table 8). TKW was positively correlated to both seed number per spike and HI under low moisture. However, under high moisture, TKW was not significantly correlated with any of agronomic traits scored (Table 8).

Table 6. Pearson correlation coefficients (for Ngamia) under low (below the diagonal) and high (above the diagonal and bold) moisture regime

	Tillers	Height	Biomass	TKW	Seed/spk	HI	WUE	YIELD
Tillers	-	0.576	0.442	0.058	0.220	0.464	0.097	0.466
Height	-0.181	-	0.745	0.511	0.683	0.915*	-0.358	0.961**
Biomass	-0.101	-0.953**	-	0.489	0.204	0.490	0.283	0.680
TKW	-0.392	0.853*	0.908*	-	0.752	0.574	-0.147	0.559
Seed/spk	0.217	0.888*	0.901*	0.645	-	0.873*	-0.706	0.749
HI	0.025	0.950**	0.985**	0.825	0.945**	-	-0.644	0.965**
WUE	-0.752	0.164	0.274	0.620	-0.149	0.143	-	-0.488
YIELD	0.102	0.943**	0.972**	0.807*	0.964**	0.994**	0.056	-

* significant at P<0.05

** Significant at P<0.001.

Table 7. Pearson correlation coefficients for Chozi under low (below the diagonal) and high (above the diagonal) moisture levels

	Tillers	Height	Biomass	TKW	Seed/spk	HI	WUE	YIELD
Tillers	-	-0.185	-0.033	-0.193	-0.429	-0.162	0.546	-0.105
Height	0.511	-	0.937**	0.312	0.729	0.805*	-0.824*	0.879*
Biomass	0.228	0.888*	-	0.138	0.824*	0.906*	-0.823*	0.958**
TKW	0.271	0.815*	0.903*	-	0.156	-0.240	-0.021	-0.115
Seed/spk	0.406	0.879*	0.932**	0.730	-	0.821*	-0.907*	0.819*
HI	0.402	0.911*	0.974**	0.943**	0.913*	-	-0.897*	0.987**
WUE	-0.676	-0.087	0.178	0.385	-0.176	0.110	-	-0.886*
YIELD	0.365	0.880*	0.969**	0.913*	0.928**	0.989**	0.088	-

* significant at P<0.05

** Significant at P<0.01.

Table 8. Pearson correlation coefficients (for Kwale) under low (below the diagonal) and high (above the diagonal and bold) moisture regime

	Tillers	Height	Biomass	TKW	Seed/spk	HI	WUE	YIELD
Tillers	-	-0.792	-0.660	-0.118	-0.706	-0.807*	0.489	-0.898*
Height	-0.070	-	0.606	-0.104	0.957**	0.966**	-0.644	0.902*
Biomass	-0.213	0.967**	-	0.717	0.424	0.620	0.128	0.815*
TKW	-0.095	0.916*	0.947**	-	-0.280	-0.023	0.697	0.259
Seed/spk	-0.105	0.950**	0.878*	0.780*	-	0.945**	-0.812*	0.816*
HI	-0.115	0.953**	0.932**	0.801*	0.957**	-	-0.651	0.945**
WUE	-0.159	0.159	0.330	0.536	-0.091	-0.006	-	-0.435
YIELD	-0.184	0.941**	0.964**	0.846*	0.905*	0.984**	0.145	-

* significant at P<0.05

** Significant at P<0.01.

4.4.5. Mbuni

The correlation coefficients of yield components with yield and water use efficiency of Mbuni are presented in Table 9. None of the traits showed a significant correlation with WUE under low moisture regimes but seeds per spike correlated negatively ($r = -0.814$) with WUE under high moisture condition (Table 9). Plant height, seeds per spike, biomass and HI showed a significant positive correlation with grain yield under both low and high moisture levels (Table 9). HI had the strongest positive correlation with yield under both low ($r = 0.970$) and high ($r = 0.999$) moisture regimes. Also, HI was positively correlated to plant height and biomass under both watering levels (Table 9).

4.4.6. Pasa

The agronomic traits studied (number of tillers per plant, plant height, biomass, TKW, seed number per spike and harvest index) did not show significant correlation with WUE under both moisture regimes (Table 10). HI, biomass, seed number per spike and plant height showed significant positive correlation with grain yield of Pasa under both high and low watering regimes (Table 10).

Table 9. Pearson correlation coefficients (for Mbuni) under low (below the diagonal) and high (above the diagonal and bold) moisture regime

	Tillers	Height	Biomass	TKW	Seed/spk	HI	WUE	YIELD
Tillers	-	0.192	0.429	-0.042	-0.130	0.002	0.286	0.020
Height	-0.274	-	0.833*	0.254	0.878*	0.899*	-0.782	0.889*
Biomass	-0.417	0.854*	-	0.470	0.817*	0.884*	-0.480	0.899*
TKW	-0.727	0.733	0.695	-	0.428	0.429	0.133	0.454
Seed/spk	-0.305	0.947**	0.794*	0.647	-	0.966**	-0.814*	0.966**
HI	-0.091	0.864*	0.800*	0.544	0.908*	-	-0.750	0.999*
WUE	-0.441	-0.009	0.219	0.445	-0.263	-0.293	-	-0.727
YIELD	-0.213	0.879*	0.915*	0.629	0.880*	0.970*	-0.084	-

* significant at P<0.05

** Significant at P<0.01.

Table 10. Pearson correlation coefficients (for Pasa) under low (below the diagonal) and high (above the diagonal and bold) moisture regime

	Tillers	Height	Biomass	TKW	Seed/spk	HI	WUE	YIELD
Tillers	-	-0.055	0.021	-0.369	-0.102	0.047	-0.356	-0.005
Height	0.056	-	0.944**	0.175	0.955**	0.984**	-0.688	0.977**
B/mass	0.081	0.597	-	0.141	0.873*	0.942**	-0.495	0.954**
TKW	0.157	0.705	0.104	-	-0.012	0.036	0.205	0.058
S/spk	-0.181	0.969**	0.525	0.658	-	0.940**	-0.737	0.919*
HI	-0.221	0.939**	0.692	0.499	0.968**	-	-0.723	0.994**
WUE	0.393	-0.108	0.558	-0.121	-0.239	-0.119	-	-0.653
YIELD	-0.108	0.827*	0.830*	0.222	0.830*	0.924**	0.111	-

* significant at P<0.05

** significant at P<0.01

4.5. Path effects of tillers per plant on water use efficiency of six wheat genotypes

4.5.1. Duma

Tiller number per plant had a strong direct positive effect (0.352) on the WUE of Duma under low moisture. This direct positive effect was boosted by the indirect, but relatively low, positive effect via biomass (0.252), plant height (0.193) and seed number per spike (0.131) giving a strong positive overall effect ($r=0.928$).

In contrast, tiller number per plant had a relatively lower direct positive effect (0.109) on WUE under high moisture. This low direct positive effect was boosted by the indirect positive effect through seed number per spike (0.091) and plant height (0.060), but was marginally counter-balanced by the indirect negative effect via biomass (-0.030).

4.5.2. Ngamia

Under low moisture, the direct positive effect (0.627) of tiller number per plant on the WUE of Ngamia was partially reinforced by the indirect effect via seed number per spike (0.136) but marginally counteracted by the indirect negative influence via plant height (-0.113) and biomass (-0.063). Consequently, the overall effect of tiller number per plant was positive and moderately strong under low moisture (Table 11).

The overall effect of tiller number per plant (-0.966) on the WUE of Ngamia was strongly negative under high moisture. This high negative effect was contributed substantially by the direct negative effect (-0.432), which was reinforced by the indirect negative effects

via plant height (-0.249), biomass (-0.191) and seed number per spike (-0.095) (Table 11).

4.5.3. Chozi

The overall positive influence (0.499) of tiller number per plant on WUE of Chozi under low moisture was contributed mainly by the direct positive effect (0.314) that was augmented by the indirect positive effects via plant height (0.160), seeds per spike (0.127) and biomass (0.072).

Under high moisture, the influence of tiller number per plant on WUE of Chozi was negative but very small (-0.047). This negative influence was as a result of the moderate direct negative (-0.133) effect that was partially counter-balanced by indirect positive effect through seed number per spike (0.057), plant height (0.025), and biomass (0.004) (Table 11).

4.5.4. Kwale

Tiller number per plant had a strong direct positive effect on WUE of Kwale under both watering regimes but the high direct positive influence of tiller number per plant was marginally counter-balanced by the indirect negative effect via biomass (-0.128), seed number per spike (-0.063) and plant height (-0.042) under low moisture (Table 11). Thus the overall effect of tiller number per plant on WUE of Kwale under low moisture was positive and moderately high (0.368).

However, under high moisture regime, the direct positive effect of tiller number per plant on WUE of Kwale was completely nullified by the high indirect negative effect via plant height (-0.356), seed number per spike (-0.317) and biomass (-0.297), which also contributed substantially to the overall strong negative effect (-0.520) (Table 11).

4.5.5. Mbuni

The high direct positive effect (0.573) of tiller number per plant on WUE of Mbuni under low moisture level was largely counter balanced by the indirect negative effect through biomass (-0.239), seed number per spike (-0.175) and plant height (-0.157), thus resulting in a very low overall positive (Table 11).

Under high moisture, the overall effect of tiller number per plant on WUE of Mbuni was negative and relatively strong (-0.569). This was mainly due to the direct negative effect (-0.285), which was reinforced by the indirect negative, but small effect through biomass (-0.147) and plant height (-0.066) and partially counter-balanced by indirect positive effect via seed number per spike (0.045) (Table 11).

4.5.6. Pasa

The direct effect of tiller number on WUE of pasa was strong and positive (0.695) under low moisture regime. This direct effect was reinforced by positive but small indirect effects via biomass and plant height, and marginally counter-balanced by negative indirect effect via seed number per spike (-0.151). Consequently, the overall effect of tiller number per plant on WUE of Pasa was strong and positive (Table 11).

Under high moisture regime, tiller number per plant maintained a positive direct effect (0.675) on WUE of Pasa. The strong direct positive influence was boosted by a small indirect positive influence via biomass (0.017) but partially counteracted by the indirect negative effect through seed number per spike (-0.083) and plant height (-0.045). Thus the overall effect of tiller number on WUE of Pasa was strong and positive (Table 11).

Table 11. Direct and indirect path effects of tillers/plant on water use efficiency of six wheat genotypes under two moisture regimes.

Cultivar	Treatment		Direct effect	Indirect effect via			Total
	Moisture regime			height	biomass	seed/spike	
Duma	Low		0.352	0.193	0.252	0.131	0.928
	High		0.109	0.060	-0.030	0.091	0.229
Ngamia	Low		0.627	-0.113	-0.063	0.136	0.587
	High		-0.432	-0.249	-0.191	-0.095	-0.966
Chozi	Low		0.314	0.160	0.072	0.127	0.449
	High		-0.133	0.025	0.004	0.057	-0.047
Kwale	Low		0.601	-0.042	-0.128	-0.063	0.368
	High		0.449	-0.356	-0.297	-0.317	-0.520
Mbuni	Low		0.573	-0.157	-0.239	-0.175	0.002
	High		-0.285	-0.066	-0.147	0.045	-0.569
Pasa	Low		0.695	0.047	0.068	-0.151	0.659
	High		0.675	-0.045	0.017	-0.083	0.564

4.6. Path effects of plant height on water use efficiency of six wheat genotypes

4.6.1 Duma

The overall effect of plant height on WUE of Duma was negative (-0.972) under low moisture. This negative effect was due to the direct negative effect (-0.283), which was boosted by the indirect negative effect of plant height via biomass (-0.267), seed number per spike (-0.267) and tiller number per plant (-0.155) (Table 12).

Under high moisture, in contrast, the overall effect of plant height on WUE of Mbuni was positive (0.972). This positive effect was mainly due to the direct positive effect (0.407), which was reinforced by indirect effect through seed number per spike (0.225), tiller number per plant (0.201) and biomass (0.139) (Table 12).

4.6.2. Ngamia

The influence of plant height on WUE of Ngamia was highly positive (0.943) under low moisture regime. This was due to direct positive effect (0.358), which was boosted by indirect positive effect via biomass (0.340) and seed number per spike (0.315) but partially counter-balanced by indirect negative effect via tiller number per plant (-0.070) (Table 12).

Under high moisture regime, the high direct positive effect of plant height on the WUE of Ngamia was reinforced by indirect positive effect through seed number per spike (0.229), biomass (0.251) and tiller number per plant (0.118) thus giving a strong positive overall effect (Table 12).

4.6.3. Chozi

The WUE of Chozi was negatively (-0.431) influenced by plant height under low moisture. This negative effect was due to low direct negative effect (-0.093) that was reinforced by indirect negative effect through biomass (-0.150) number of seeds per spike (-0.141) and tillers/plant (-0.047) (Table 12).

Under high moisture, plant height had a positive overall effect on the WUE of Chozi. This was mainly due to the positive direct effect (0.519), which was augmented by indirect positive effect through biomass (0.391) and tiller number per plant (0.096) but counter-balanced partially by indirect negative effect via seeds per spike (-0.379) (Table 12).

4.6.4. Kwale

The influence of plant height on WUE of Kwale was negative (-0.950) under low moisture regime. The relatively high negative overall effect of plant height on WUE of Kwale was mainly due to the high direct negative (-0.364) effect, which was reinforced by indirect negative effect via biomass (-0.332) and seed number per spike (-0.326) (Table 12).

Similarly, under high moisture, WUE of Kwale was negatively (-0.849) influenced by plant height. The relatively high negative effect was due to direct (-0.480) and indirect negative effects via seed number per spike (-0.459) and biomass (-0.291), which was,

however, partially counter-balanced by indirect positive effect through tiller number per plant (0.380) (Table 12).

4.6.5. Mbuni

Plant height had a positive effect (0.998) on WUE of Mbuni under low moisture. The high positive effect was mainly due to the high direct positive (0.415) effect. In addition, seed number per spike (0.418) and biomass (0.391) contributed indirectly to WUE of Mbuni. However, plant height had detrimental effects (-0.157) on WUE indirectly via tiller number per plant (Table 12).

In contrast, plant height had a negative influence (-0.990) on WUE of Mbuni under high moisture. This negative effect was due to the high direct negative effect (-0.392), which was augmented by indirect negative effect via seed number per spike (-0.281) and biomass (-0.264) (Table 12).

4.6.6. Pasa

Water use efficiency of Pasa was influenced negatively (-0.797) by plant height under low moisture. The overall negative effect of plant height on WUE of Pasa was due to direct negative effect (-0.304) that was supported by indirect negative effect via seed number per spike (-0.295) and biomass (-0.182) (Table 12).

Under high moisture regime, WUE of Pasa was similarly effected negatively (-0.991) by plant height. The overall negative effect was mainly due to the direct (-0.352) effect that

was reinforced by the indirect negative effect through seed number per spike (-0.333) and biomass (-0.329) but marginally reduced by the indirect positive effect through tiller number per plant (0.025) (Table 12).

Table 12. Direct and indirect path effects of plant height on water use efficiency of six wheat genotypes under two moisture regimes.

Treatment		Direct effect	Indirect effect via			Total
Cultivar	Moisture regime		tiller/plant	biomass	seed/spike	
Duma						
	Low	-0.283	-0.155	-0.267	-0.267	-0.972
	High	0.407	0.201	0.139	0.225	0.972
Ngamia						
	Low	0.358	-0.070	0.340	0.315	0.943
	High	0.378	0.118	0.251	0.229	0.976
Chozi						
	Low	-0.093	-0.047	-0.150	-0.141	-0.431
	High	0.519	0.096	0.391	-0.379	0.628
Kwale						
	Low	-0.364	0.072	-0.332	-0.326	-0.950
	High	-0.480	0.380	-0.291	-0.459	-0.849
Mbuni						
	Low	0.415	-0.157	0.391	0.418	0.998
	High	-0.392	-0.053	-0.264	-0.281	-0.990
Pasa						
	Low	-0.304	-0.017	-0.182	-0.295	-0.797
	High	-0.352	0.025	-0.329	-0.333	-0.991

4.7. Path effects of biomass on water use efficiency of six wheat genotypes

4.7.1. Duma

Biomass had a fairly low negative influence on WUE of Duma under low moisture. This low negative effect was attributed to the relatively low direct negative effect (-0.048), and indirect negative effect through plant height (-0.045), seed number per spike (-0.044) and tiller number per plant (-0.034) (Table 13).

Under high moisture regime, in contrast, biomass had a low positive effect (0.038) on WUE of Duma. This overall positive effect was due to direct but low positive effect (0.028), which was reinforced by indirect positive effects via plant height (0.011) and seed number per spike (0.007) but partially counterbalanced by detrimental indirect effect via tiller number per plant (-0.008) (Table 13).

4.7.2. Ngamia

The effect of biomass on WUE of Ngamia was positive and strong under low moisture. This strong positive influence of biomass was due to direct positive effect (0.355), which was enhanced by indirect positive contribution through plant height (0.338) and seed number per spike (0.320) but marginally reduced by indirect negative effect via tiller number per plant (-0.035) (Table 13).

Under high moisture, the effect of biomass on WUE of Ngamia was similarly positive but very low. This low overall effect was due to low direct positive influence (0.082), which

was reinforced by equally low indirect positive effect via tiller number per plant (0.036), plant height (0.061) and seed number per plant (0.017) (Table 13).

4.7.3. Chozi

The relatively high positive overall (0.805) influence of biomass on WUE of Chozi under low moisture was attributed to the direct positive effect (0.264), which was enhanced by indirect positive contribution through seed number per spike (0.246), plant height (0.235) and tiller number per plant (0.060) (Table 13).

Similarly, the effect of biomass on WUE of Chozi was highly positive (0.874) under high moisture. This high positive influence of biomass was due to moderately high direct positive effect (0.401) that was augmented by indirect effect via seed per spike (0.276) and plant height (0.263) but marginally reduced by the indirect negative effect via tiller number per plant (-0.066) (Table 13).

4.7.4. Kwale

Water use efficiency of Kwale was negatively influenced by biomass under low moisture. The strong negative influence of biomass on WUE was attributed to moderately high direct negative effect (-0.425) that was reinforced by indirect effect via seed number per spike (-0.291) and plant height (-0.285) but partially counter-balanced by the indirect positive effect via tiller number per plant (0.010) (Table 13).

Under high moisture, however, biomass positively (0.214) influenced WUE of Kwale. The high direct positive influence (0.571) was reinforced by an indirect positive effect via seed number per spike (0.363) but partially counter-balanced by indirect negative effect via tiller number per plant (-0.377) and plant height (-0.343) (Table 13).

4.7.5. Mbuni

The high overall negative effect (-0.843) of biomass on WUE of Mbuni at low moisture level was due to the high direct negative effect (-0.420), which was reinforced by indirect negative effect via plant height (-0.318) and seed number per spike (-0.289) but partially counter balanced by indirect positive effect via tiller number per plant (0.184) (Table 13).

Under high moisture, however, biomass had a positive but low influence (0.030) on WUE of Mbuni. This overall positive effect was due to both direct (0.010) and indirect contributions via plant height (0.008), seed number per spike (0.008) and tiller number per plant (0.004) (Table 13).

4.7.6. Pasa

Biomass had a strong positive effect (0.800) on WUE of Pasa at low moisture level. This strong effect was attributed to the relatively high direct positive effect (0.363), which was reinforced by indirect effect via plant height (0.217), seed number per spike (0.191) and Tiller number per plant (0.059) (Table 13). Biomass also had a positive effect (0.292) on WUE of pasa under high moisture which was attributed to both direct (0.103) and indirect positive effects via plant height (0.097), seed number per spike (0.090) and tillers per plant (0.002) (Table 13).

Table 13. Direct and indirect path effects of biomass on water use efficiency of six wheat genotypes under two moisture regimes

Treatment		Direct effect	Indirect effect via			Total
Cultivar	Moisture regime		tiller/plant	plant height	seed/spike	
Duma						
	Low	-0.048	-0.034	-0.045	-0.044	-0.171
	High	0.028	-0.008	0.011	0.007	0.038
Ngamia						
	Low	0.355	-0.035	0.338	0.320	0.976
	High	0.082	0.036	0.061	0.017	0.196
Chozi						
	Low	0.264	0.060	0.235	0.246	0.805
	High	0.401	-0.066	0.263	0.276	0.874
Kwale						
	Low	-0.425	0.010	-0.285	-0.291	-0.991
	High	0.571	-0.377	-0.343	0.363	0.214
Mbuni						
	Low	-0.420	0.184	-0.318	-0.289	-0.843
	High	0.010	0.004	0.008	0.008	0.030
Pasa						
	Low	0.363	0.059	0.217	0.191	0.800
	High	0.103	0.002	0.097	0.090	0.292

4.8. Path effects of number of seeds per spike on water use efficiency of six wheat genotypes

4.8.1. Duma

Number of seeds per spike had a strong positive influence on WUE of Duma at low moisture level. This was due to the direct positive effect (0.263), which was boosted by indirect positive effect via plant height (0.248), biomass (0.238) and tillers per plant (0.098) (Table 14).

Under high moisture, in contrast, the effect of number of seeds per spike on WUE of Duma was negative (-0.750). The relatively high overall negative effect was attributed mainly to the direct negative effect (-0.259), which was boosted by indirect negative effect via tiller number per plant, plant height and biomass (Table 14).

4.8.2. Ngamia

The effect of number of seeds per spike on WUE of Ngamia was positive but very weak (0.013) under low moisture. This was due to both weak direct (0.004), and indirect effects via plant height (0.004), biomass (0.004) and tiller number per plant (0.001) (Table 14).

Similarly, under high moisture the effect of number of seeds per spike on WUE of Ngamia was positive (0.733) and this influence was mainly due to direct negative effect (0.348), which was reinforced by indirect contributions via tiller number per plant (0.077), plant height (0.238) and biomass (0.071) (Table 14).

4.8.3. Chozi

Water use efficiency of Chozi was affected negatively by seed number per spike under both low and high moisture. The overall negative effect (-.855) of seed number per spike on WUE, under low moisture, was contributed both direct (-0.266) and indirect effects via biomass (-0.248), plant height (-0.234) and tiller number per plant (-0.108) (Table 14). However, under high moisture, the overall negative effect of number of seed number per spike was attributed to direct effect. This was reinforced by indirect effect via biomass (-0.390) and plant height (-0.345). Ultimately the negative effect was partially counter-balanced by the indirect positive effect via tiller number per plant (0.203) (Table 14).

4.8.4. Kwale

Seed number per spike negatively influenced WUE of Kwale under both low and high moisture regimes. The high overall negative effect (-0.991) of seed number per spike on WUE under low moisture was due to the relatively high direct negative effect (-0.368), which was reinforced by indirect negative effect via tiller number per plant (-0.039) plant height (-0.311) and biomass (-0.273) (Table 14).

Under high moisture, the negative overall effect (-0.649) of seed number per spike was due to direct negative effect, which was augmented by indirect negative effects via biomass (-0.292) and plant height (-0.158) but partially counter-balanced by the indirect positive effect via tiller number per plant (0.488) (Table 14).

4.8.5. Mbuni

The effect of seed number per spike on WUE of Mbuni was negative and strong (-0.973) at low moisture level. This strong negative effect was due to direct effect that was enhanced by indirect negative effects via plant height (-0.379) and biomass (-0.317) but partially counter-balanced by indirect positive effect via tiller number per plant (0.122) (Table 14).

Under high moisture regime, the relatively high negative influence (-0.692) of seed number per spike resulting from the direct negative effect. This was reinforced by indirect negative effect via plant height (-0.237) and biomass (-0.220) but partially counter-balanced by indirect positive effect via tiller number per plant (0.035) (Table 14).

4.8.6. Pasa

Seed number per spike had a strong positive effect (0.992) on WUE of Pasa under low moisture. The high overall positive influence was due to high direct positive effect (0.485), which was reinforced by indirect positive effect via plant height (0.390) and biomass (0.215) but partially counteracted by indirect negative effect through tiller number per plant (-0.098).

Under high moisture, seed number per spike influenced WUE of Pasa negatively (-0.829). Both direct and indirect effects contributed to this relatively high negative effect. The direct negative effect (-0.396) was enhanced by indirect negative effect via plant

height (-0.298) and biomass (-0.276) but partially counter-balanced by indirect positive effect via tiller number per plant (0.141) (Table 14).

Table 14. Direct and indirect path effects of seed number per spike on water use efficiency of six wheat genotypes under two moisture regimes

Treatment		Direct effect	Indirect effect via			Total
Cultivar	Moisture regime		tiller/plant	plant height	biomass	
Duma						
	Low	0.263	0.098	0.248	0.238	0.847
	High	-0.259	-0.217	-0.214	-0.061	-0.750
Ngamia						
	Low	0.004	0.001	0.004	0.004	0.013
	High	0.348	0.077	0.238	0.071	0.733
Chozi						
	Low	-0.266	-0.108	-0.234	-0.248	-0.855
	High	-0.474	0.203	-0.345	-0.390	-0.986
Kwale						
	Low	-0.368	-0.039	-0.311	-0.273	-0.991
	High	-0.688	0.488	-0.158	-0.292	-0.649
Mbuni						
	Low	-0.400	0.122	-0.379	-0.317	-0.973
	High	-0.270	0.035	-0.237	-0.220	0.692
Pasa						
	Low	0.485	-0.098	0.390	0.215	0.992
	High	-0.396	0.141	-0.298	-0.276	-0.829

4.9. Path effects of tiller number per plant on grain yield of six wheat genotypes

4.9.1. Duma

The effect of tiller number per plant on the yield of Duma was positive (0.857) at low moisture level. The high overall positive influence was due to the direct positive effect (0.325), which was boosted by indirect positive effects via biomass (0.232), plant height (0.179) and seed number per spike (0.121) (Table 15).

In contrast, under high moisture regime tiller number per plant had a negative but low effect (-0.017) on the yield of Duma. This low negative effect came as a result of direct low negative effect (-0.008), which was enhanced by indirect negative effects through seed number per spike (-0.007) and plant height (-0.004) but counteracted by indirect positive effect through biomass (0.002) (Table 15).

4.9.2. Ngamia

Tiller number per plant had a strong positive effect (0.919) on yield of Ngamia under low moisture, which was contributed by both direct (0.352), and indirect positive effects via biomass (0.252), plant height (0.193) and seed number per spike (0.122) (Table 15).

Under high moisture regime, however, tiller number per plant influenced grain yield of Ngamia negatively (-0.058). The overall negative influence was due to direct negative, albeit, low effect (-0.026), which was enhanced by indirect negative effects via plant height (-0.015), biomass (-0.011) and seed number per spike (-0.006) (Table 15).

4.9.3. Chozi

The effect of tiller number per plant on yield of Chozi was negative (-0.777) under low moisture. This strong negative effect resulted from the high direct negative effect (-0.362) that was boosted by indirect negative effects via plant height (-0.185), seed number per spike (-0.147) and biomass (-0.083) (Table 15).

Under high moisture, however, tiller number per plant influenced the yield of Chozi positively (0.138). This positive, but low influence was due to the direct positive effect (0.390) that was partially counteracted by indirect negative effects through seed number per spike (-0.167), plant height (-0.072) and biomass (-0.013) (Table 15).

4.9.4. Kwale

Tiller number per plant had a positive effect (0.669) on yield of Kwale under low moisture, which was due to both direct positive influence (0.482), and indirect positive influence via biomass (0.103), seed number per spike (0.051) and plant height (0.034) (Table 15).

Under high moisture, in contrast, tiller number per plant influenced the yield of Kwale negatively (-0.213) since the direct positive effect (0.184) was completely counterbalanced by indirect negative effects via plant height (-0.146), seed number per spike (-0.130) and biomass (-0.121) (Table 15).

4.9.5. Mbuni

The effect of tiller number per plant on the grain yield of Mbuni was positive (0.423) under low moisture. This positive effect was contributed mainly by high indirect positive effects via biomass (0.337), seed number per spike (0.266) and plant height (0.246) as the direct effect was negative and relatively high (-0.426) (Table 15).

Under high moisture, tiller number per plant similarly had a positive effect (0.735) on the yield of Mbuni. This positive influence was mainly due to the direct positive effect (0.480) that was reinforced by indirect positive effect via biomass (0.206) and plant height (0.092) but partially counter-balanced by indirect negative effect via seed number per spike (-0.043) (Table 15).

4.9.6. Pasa

The effect of tiller number per plant on the yield of Pasa was positive (0.312) under low moisture. This positive influence was mainly due to the direct effect (0.327), which was reinforced by indirect positive effect through biomass (0.026) and plant height (-0.018) but partially counteracted by indirect negative effect via seed number per spike (-0.059) (Table 15).

However, under high moisture, tiller number per plant influenced yield of Pasa negatively (-0.402). The negative overall influence was due to the direct negative effect (-0.466) that was reinforced by indirect negative effect via biomass (-0.010) but marginally

counter-balanced by indirect positive effect via seed number per spike (0.048) and plant height (0.026).

Table 15. Direct and indirect path effects of tillers/plant on grain yield of six wheat genotypes under two moisture regimes.

Treatment		Direct effect	Indirect effect via			Total
Cultivar	Moisture regime		plant height	biomass	seed/spike	
Duma						
	Low	0.325	0.179	0.232	0.121	0.857
	High	-0.008	-0.004	0.002	-0.007	-0.017
Ngamia						
	Low	0.352	0.193	0.252	0.122	0.919
	High	-0.026	-0.015	-0.011	-0.006	-0.058
Chozi						
	Low	-0.362	-0.185	-0.083	-0.147	-0.777
	High	0.390	-0.072	-0.013	-0.167	0.138
Kwale						
	Low	0.482	0.034	0.103	0.051	0.670
	High	0.184	-0.146	-0.121	-0.130	-0.213
Mbuni						
	Low	-0.426	0.246	0.337	0.266	0.423
	High	0.480	0.092	0.206	-0.043	0.735
Pasa						
	Low	0.327	0.018	0.026	-0.059	0.312
	High	-0.466	0.026	-0.010	0.048	-0.402

4.10. Path effects of plant height on yield of six wheat genotypes

4.10.1. Duma

Plant height had a strong positive effect (0.808) on the yield of Duma under low moisture as a result of the direct positive effect (0.235) that was boosted by indirect positive effect via number of seed number per spike (0.222), biomass (0.222) and tiller number per plant (0.129) (Table 16).

Under high moisture, however, plant height had a negative effect (-0.301) on the yield of Duma. This was due to direct negative effect (-0.132), which was enhanced by indirect negative effects via number of seed number per spike (-0.109) and biomass (-0.053) but marginally counter-balanced by an indirect positive effect through number of tiller number per plant (0.007) (Table 16).

4.10.2. Ngamia

The effect of plant height on grain yield of Ngamia was positive under both low (0.911) and high (0.876) watering regimes. Under low moisture, the positive influence of plant height on yield was due to direct positive effect (0.483), which was augmented by indirect positive effect via biomass (0.318) and seed number per spike (0.290) but partially counteracted by indirect negative effect via tiller number per plant (-0.180) (Table 16).

Under high moisture, the positive effect of plant height on yield of Ngamia was due to both direct positive effect (0.292), and indirect effect positive effect via biomass (0.217), seed number per spike (0.199) and tiller number per plant (0.118) (Table 16).

4.10.3. Chozi

Plant height had a positive, albeit, low effect (0.269) on the grain yield of Chozi under low moisture. This overall positive effect was due to the direct positive effect (0.082), which was reinforced by indirect positive effect via biomass (0.073), seed number per spike (0.072) and number of tiller number per plant (0.042) (Table 16).

Under high moisture, in contrast, the effect of plant height on the grain yield of Chozi was positive and strong (0.967). This was due to the direct positive influence (0.374), which was reinforced by strong indirect positive effect via biomass (0.375) and seed number per spike (0.292) but partially counteracted by indirect negative effect via tillers per plant (-0.074) (Table 16).

4.10.4. Kwale

Plant height had detrimental effect (-0.865) on the yield of Kwale under low moisture. This detrimental effect was due to direct negative effect (-0.304), which was enhanced by indirect negative effect via biomass (-0.294) and seed number per spike (-0.289) but marginally counterbalanced by indirect positive effect via tiller number per plant (0.021) (Table 16).

However, plant height had a strong positive influence (0.855) on yield of Kwale under high moisture. The positive effect was due to direct positive effect (0.483) that was augmented by indirect positive effect via seed number per spike (0.462) and biomass (0.293) but partially counterbalanced by indirect negative effect through tiller number per plant (-0.383) (Table 16).

4.10.5. Mbuni

Plant height had detrimental effect (-0.665) on the grain yield of Mbuni under low moisture. This detrimental effect was due to direct negative effect (-0.263) that was reinforced by indirect negative effect via seed number per spike (-0.249) and biomass (-0.225) but partially counterbalanced by indirect positive effect through tiller number per plant (0.072) (Table 16).

The effect of plant height on grain yield of Mbuni was, however, positive (0.954) under high moisture. The high positive influence was due to both direct positive effect (0.416), and indirect positive effect via biomass (0.253), seed number per spike (0.205) and tiller number per plant (0.080) (Table 16).

4.10.6. Pasa

Plant height had a negative effect (-0.472) on the grain yield of Pasa under low moisture, which was due to both direct negative effect (-0.180), and indirect negative effect via seed number per spike (-0.175), biomass (-0.107) and tiller number per plant (-0.010) (Table 16).

The effect of plant height on grain yield of Pasa was similarly detrimental (-0.0673) under high moisture. The negative effect of plant height on the yield of Pasa was contributed by direct negative effect (-0.237) that was augmented by indirect negative effect via seed number per spike (-0.226) and biomass (-0.224) but partially counteracted by indirect positive effect via tillers per plant (0.013) (Table 16).

Table 16. Direct and indirect path effects of plant height on yield of six wheat genotypes under two moisture regimes.

Treatment		Direct effect	Indirect effect via			Total
Cultivar	Moisture regime		tillers/plant	biomass	seed/spike	
Duma						
	Low	0.235	0.129	0.222	0.222	0.808
	High	-0.132	0.007	-0.053	-0.109	-0.301
Ngamia						
	Low	0.483	-0.180	0.318	0.290	0.911
	High	0.292	0.118	0.217	0.199	0.876
Chozi						
	Low	0.082	0.042	0.073	0.072	0.269
	High	0.374	-0.074	0.375	0.292	0.967
Kwale						
	Low	-0.304	0.021	-0.294	-0.289	-0.865
	High	0.483	-0.383	0.293	0.462	0.855
Mbuni						
	Low	-0.263	0.072	-0.225	-0.249	-0.665
	High	0.416	0.080	0.253	0.205	0.954
Pasa						
	Low	-0.180	-0.010	-0.107	-0.175	-0.472
	High	-0.237	0.013	-0.224	-0.226	-0.673

4.11. Path effects of biomass on yield of six wheat genotypes

4.11.1. Duma

Biomass had a strong positive effect (0.873) on the yield of Duma at low moisture level, which was contributed by direct positive effect (0.245), and indirect positive effect via plant height (0.231), seed number per spike (0.222) and tiller number per plant (0.175) (Table 17).

The effect of biomass on grain yield of Duma was similarly positive, but very low, under high moisture. This was due to the low direct positive effect (0.010), which was boosted by equally low indirect positive effect via plant height (0.002) and seed number per spike (0.001) but marginally counterbalanced by indirect negative effect via tiller number per plant (-0.001) (Table 17)

4.11.2. Ngamia

The yield of Ngamia was positively influenced (0.893) by biomass at low moisture level. This was through direct positive contribution of biomass as well as indirect positive contribution via plant height (0.308) and seed number per spike (0.292) but marginally counterbalanced by indirect negative effect via tiller number per plant (-0.033) (Table 17).

Under high moisture, however, biomass had a negative effect (-0.616) on the grain yield of Ngamia. This negative effect was contributed by direct negative effect (-0.258) as

well as indirect negative effects via plant height (-0.192), tiller number per plant (-0.114) and seed number per spike (-0.053) (Table 17).

4.11.3. Chozi

Biomass had a strong positive effect (0.994) on the grain yield of Chozi under low watering regime. This high positive effect was contributed by both direct positive effect (0.368), and indirect positive effect via plant height (0.274), seed number per spike (0.261) and tiller number per plant (0.091) (Table 17).

At high moisture level, however, the effect of biomass on the grain yield of Chozi was negative. The strong negative effect (-0.971) was due to the relatively high direct negative effect (-0.478), which was reinforced by indirect negative effect via plant height (-0.367) and seed number per spike (-0.303) but partially reduced by indirect positive effect via tiller number per plant (0.177) (Table 17).

4.11.4. Kwale

The effect of biomass on the grain yield of Kwale was positive under low moisture regime. The relatively high positive influence was due to direct positive effect (0.257), which was enhanced by indirect positive effect via plant height (0.248) and seed number per spike (0.225) but marginally counteracted by indirect negative effect via tiller number per plant (-0.055) (Table 17).

The effect of biomass on the grain yield of Kwale was similarly positive, albeit low, (0.341) at high moisture level. This was due to direct positive effect (0.249), which was reinforced by indirect positive effect via plant height (0.151) and seed number per spike (0.105) but partially counteracted by indirect negative effect via number of tiller number per plant (-0.164) (Table 17).

4.11.5. Mbuni

The overall effect of biomass on the grain yield of Mbuni was positive (0.629) at low moisture level. This was due to the direct positive effect (0.282), which was augmented by indirect positive influence via plant height (0.241) and seed number per spike (0.224) but partially reduced by indirect negative effect via tiller number per plant (-0.118) (Table 17).

However, under high moisture, the effect of biomass was negative, but very low (-0.008). This was due to the low direct negative effect (-0.003) and low indirect negative effect via plant height (-0.002), seed number per spike (-0.002) and tiller number per plant (-0.001) (Table 17).

4.11.6. Pasa

Biomass had a positive effect (0.350) on the grain yield of Pasa under low moisture regime and this was due to both direct positive contribution (0.159), and indirect positive influence via plant height (0.095), seed number per spike (0.083) and tiller number per plant (0.013) (Table 17).

The effect of biomass on grain yield of Pasa was similarly positive (0.932) under high watering regime, and this was due to direct positive contribution (0.397) as well as indirect positive contribution via plant height (0.254), seed number per spike (0.196) and tiller number per plant (0.085) (Table 17).

Table 17. Direct and indirect path effects of biomass on the grain yield of six wheat genotypes under two moisture regimes.

Treatment		Direct effect	Indirect effect via			Total
Cultivar	Moisture regime		tillers/plant	plant height	seed/spike	
Duma						
	Low	0.245	0.175	0.231	0.222	0.873
	High	0.010	-0.001	0.002	0.001	0.012
Ngamia						
	Low	0.324	-0.033	0.308	0.292	0.893
	High	-0.258	-0.114	-0.192	-0.053	-0.616
Chozi						
	Low	0.368	0.091	0.274	0.261	0.994
	High	-0.478	0.177	-0.367	-0.303	-0.971
Kwale						
	Low	0.257	-0.055	0.248	0.225	0.675
	High	0.249	-0.164	0.151	0.105	0.341
Mbuni						
	Low	0.282	-0.118	0.241	0.224	0.629
	High	-0.003	-0.001	-0.002	-0.002	-0.008
Pasa						
	Low	0.159	0.013	0.095	0.083	0.350
	High	0.397	0.085	0.254	0.196	0.932

4.12. Path effects of seed number per spike on grain yield of six wheat genotypes

4.12.1. Duma

The effect of number of seeds per spike on grain yield of Duma was strong and positive (0.873) under low moisture. Direct positive effect (0.245) and indirect positive effect via biomass (0.222), plant height (0.231) and tiller number per plant (0.093) contributed to this strong positive effect (Table 18).

Under high moisture, in contrast, seed number per spike had a positive effect (0.012) on the grain yield of Duma. This low positive effect was due to relatively low direct positive effect (0.010) that was reduced further by indirect negative effect via tiller number per plant (-0.001).

4.12.2. Ngamia

Seed number per spike had a higher overall positive effect on yield of Ngamia under low (0.893) while it was negative (-0.617) under high moisture regime. The positive effect of seed number per spike on yield under low moisture was due to direct positive effect (0.324), and indirect positive effect via biomass (0.292) and plant height (0.308). The overall positive effect was further counteracted by the negative effect of tillers per plant (-0.033) (Table 18).

At high moisture level, the negative effect of seed number per spike was similarly due to direct negative effect (-0.258) reinforced further by the indirect negative effect via plant

height (-0.192), tiller per plant (-0.114), plant height (-0.192) and biomass (-0.053) (Table 18).

4.12.3. Chozi

Seed number per spike had a positive effect (0.994) on the yield of Chozi under low moisture. This strong positive effect was due to direct positive effect (0.368), which was reinforced by indirect positive effect via plant height (0.274), biomass (0.261) and tiller number per plant (0.091) (Table 18).

However, the effect of seed number per spike on grain yield of Chozi was negative (-0.971) at high moisture level. This was due to high direct negative effect (-0.478), which was enhanced by indirect negative effect via biomass (-0.303) and plant height (-0.367) but partially counteracted by indirect positive effect via tillers per plant (0.177) (Table 18).

4.12.4. Kwale

Seed number per spike positively influenced (0.675) grain yield of Kwale under low moisture regime and this effect was reinforced further by the direct positive effect (0.257) and indirect positive effects via plant height (0.248) and biomass (0.225) (Table 18).

Under high moisture, however, seed number per spike influenced grain yield of Kwale positively (0.341). The relatively low overall positive effect was due to the low direct positive effect (0.249), which was reinforced by indirect positive effect via plant height

(0.151) and biomass (0.105) but marginally reduced by indirect negative effect via tiller number per plant (-0.164) (Table 18).

4.12.5. Mbuni

The effect of seed number per spike on grain yield of Mbuni was positive (0.629) at low moisture level. This positive effect was due to direct positive effect (0.282), which was enhanced by indirect positive effect via plant height (0.241) and biomass (0.224) but partially counteracted by indirect negative effect of tiller number per plant (-0.118) (Table 18).

Under high moisture, in contrast, seed number per spike had a relatively low negative effect (-0.008) on grain yield of Mbuni. The overall negative effect was due to direct negative effect (-0.003) that was enhanced by indirect negative effect via plant height (-0.001), biomass (-0.002) and tiller number per plant (-0.001) (Table 18).

4.12.6. Pasa

Seed number per spike had a positive effect (0.350) on the grain yield of Pasa under low watering regime, which was contributed by direct positive effect (0.159) and reinforced further by the indirect positive effect via plant height (0.095), tiller number per plant (0.013) and biomass (0.083) (table 18).

Seed number per spike similarly had a positive effect (0.932) on grain yield of Pasa at high moisture level. This was due to high direct positive effect (0.397), which was

enhanced by indirect positive effect via plant height (0.254), biomass (0.196) and tiller number per plant (0.085) (Table 18).

Table 18. Direct and indirect path effects of seed number per spike on yield of six wheat genotypes under two moisture regimes over seasons

Treatment		Direct effect	Indirect effect via			Total
Cultivar	Moisture regime		tillers/plant	plant height	biomass	
Duma						
	Low	0.245	0.175	0.231	0.222	0.873
	High	0.010	-0.001	0.002	0.001	0.012
Ngamia						
	Low	0.324	-0.033	0.308	0.292	0.893
	High	-0.258	-0.114	-0.192	-0.053	-0.616
Chozi						
	Low	0.368	0.091	0.274	0.261	0.994
	High	-0.478	0.177	-0.367	-0.303	-0.971
Kwale						
	Low	0.257	-0.055	0.248	0.225	0.675
	High	0.249	-0.164	0.151	0.105	0.341
Mbuni						
	Low	0.282	-0.118	0.241	0.224	0.629
	High	-0.003	-0.001	-0.002	-0.002	-0.008
Pasa						
	Low	0.159	0.013	0.095	0.083	0.350
	High	0.397	0.085	0.254	0.196	0.932

5.0. DISCUSSION

5.1. Varietal Differences in Grain Yield, Water Use and Water Use Efficiency at Low and High Moisture Levels.

Generally the wheat genotypes tested yielded less under low moisture than under high moisture regime as expected. The yield levels reported in this study under low moisture regime are relatively lower than average yields under rainfed conditions in the high potential areas (such as Timau, Mau Narok and Njoro). However, the yields achieved under high moisture regime are comparable to those reported under field conditions in the high potential areas (that receive rainfall of about 1000 mm per annum). Average yields of about 2500 kg ha⁻¹ and 1500 kg ha⁻¹ have been reported for high and low potential areas, respectively (NPBRC Report, 2002). Moreover, the yields obtained in the are comparable to those reported by Kimurto *et al* (2000) under rain-shelter in Njoro.

There was a significant interaction between watering regime and cultivar on grain yield such that the drought tolerant cultivars (Duma, Ngamia and Chozi) gave greater yields than the drought susceptible ones (Kwale, Mbuni and Pasa) under low watering regime while the drought susceptible cultivars gave greater yields than the tolerant ones at high moisture level. These differences in response of grain yield to genotype and moisture regime could be due to differences in growth parameters recorded in this study. For example, drought tolerant varieties, had less number of tillers and were shorter than the drought susceptible ones under low moisture while the converse was true under high moisture regime. It is likely that at low moisture level plants experienced water stress

and therefore less number of tillers were important for reducing competition for water. Moreover, shorter plants could be due to preferential partitioning of dry matter into grain yield formation rather than just increasing the total biomass. Similar results have been recorded elsewhere. In Australia, for instance, Rebetzke *et al.* (2001) reported that wheat varieties with tiller inhibition genes resulted into increased grain yield under moisture stress environment. Ehlig and Le Mert (1976) and Singh *et al.* (1979) have also reported less number of tillers per plant for drought tolerant wheat. Besides, reduced maximum tiller number of *Triticum tauschii* was reported under low moisture (Cone *et al.*, 1995). In a hydroponics study in Australia, Blum and Sullivan (1997) found that shorter wheat plants were more drought tolerant than taller ones.

Seed number per spike and TKW did not seem to be important in affecting grain yield in this study. This is in contrast to findings by Guttieri *et al.* (2001) that the overall moisture deficit induced reduction in yield of specific wheat cultivars is largely due to its adverse effects on kernels per spike. Moreover, Kimurto (personal communication, 2002) attributed higher yields of drought tolerant varieties (Chozi and Duma) to higher kernel weight. Solomon *et al.* (2003) also attributed good performance of certain wheat varieties grown under stressed conditions in a greenhouse to higher kernel weight.

The effect of watering regime and cultivar on total crop water use was subject to interaction such that the increase in water use due to high watering regime was greater for drought sensitive than for drought tolerant varieties. These differences in water use could be attributed to the observed differences in growth parameters. For example, under high

moisture the drought susceptible varieties had more tillers per plant, relatively taller plants and higher seed number per spike. The high number of tillers per plant coupled with taller plants (for drought susceptible varieties) possibly led to a large crop canopy under high moisture regime. A large canopy may result in increased crop water use by increasing the transpiration component of the crop water balance through increased soil water extraction. Effects of a large crop canopy on total crop water use have also been reported in maize (Ogola *et al.*, 2002; Howell *et al.*, 1998; Fernández *et al.*, 1996). Under low moisture, in contrast, the drought tolerant varieties probably had more extensive root distribution than the drought susceptible ones leading to almost similar total crop water use between the two groups despite the fact that the drought tolerant varieties had less number of tillers. These results compare favourably with those of Sharp (1990) who reported that more extensive and dense root system is an indicator of drought tolerance as it leads to efficient extraction of water thus ensuring the maintenance of plant turgor and hence high transpiration and yield.

The interaction between variety and moisture regime affected water use efficiency such that drought tolerant cultivars had greater water use efficiency than drought susceptible varieties under low moisture regime while the converse was true at high moisture level. The higher WUE values for drought tolerant cultivars under low moisture is likely to be as a result of the observed greater yield of these varieties at low moisture level even though total crop water use appeared to be similar between the drought tolerant and drought susceptible varieties. One possible explanation for this is that the drought tolerant varieties may have had a lower direct evaporation of water from soil beneath the

crop canopy, E_{sc} . Since E_{sc} is largely a wasteful loss of water, a reduction in E_{sc} should lead to an increase in WUE and/or ensure more water is available for crop transpiration. For example, Lewis and Thurling (1994) in a study of three oilseed *Brassica* species in a water-limited environment, observed higher water use efficiency values in a species where soil evaporation comprised a smaller proportion of ET. Ogola *et al.* (2002) also attributed higher water efficiencies of maize (due to N application) to a reduction in E_{sc} and a concurrent increase in T. Similar results have been reported in barley (Cooper *et al.*, 1987; Shepherd *et al.*, 1987).

Similarly, the higher WUE values for drought susceptible varieties at high moisture level could be due to the observed greater yield of these varieties under high moisture regime. Although high moisture regime increased both grain yield and total crop water use, the increase in grain yield was greater than the increase in total crop water use. It is likely therefore that the increase in total crop water use was dominated by an increase in the transpiration rather than the E_{sc} component of crop water balance.

5.2. Varietal differences in growth parameters under two moisture levels.

The number of tillers per plant was affected by an interaction between moisture regime and varieties such that high moisture regime increased average tiller number per plant of drought tolerant varieties but decreased average number of tillers per plant of drought susceptible varieties. This may be a very useful attribute of drought tolerant cultivars as it implies a wide adaptability across varying environments and hence more stable yields.

For example, under water stress environments they may conserve water by developing few tillers but where water is not limiting, they may increase their yields through an increase in the number of reproductive tillers. Ehlig and Le Mert (1976) have also reported lower tiller number per plant for drought tolerant wheat while Cone *et al.* (1995) found that maximum tiller number of *Triticum tauschii* (wild relative of wheat) was strongly reduced by low moisture condition.

Drought tolerant cultivars were taller than the drought sensitive ones under high moisture. However, under low moisture the drought tolerant cultivars were generally shorter than the sensitive ones. It is likely that under low moisture regime the plants experienced considerable water stress. Short plants may do well under water stress conditions by reducing the competition for water but maintaining good yields through increased HI (mainly through better partitioning of dry matter). Similar results have been reported elsewhere. For example, Blum and Sullivan (1997) while evaluating the effect of plant size on wheat response to agents of drought under hydroponics systems in Australia found that shorter plants were more drought tolerant. Nonetheless, while genetic gain in grain yield has been achieved mainly by reducing plant height with use of dwarfing genes, an alternative method is to transfer larger amounts of the C assimilated prior anthesis to the grain during the grain filling period (Austin *et al.*, 1980).

On average, drought tolerant varieties gave lower TKW than drought sensitive ones at low moisture level although Chozi (drought tolerant cultivar) had the highest TKW across moisture regimes. This observation is not in agreement with earlier findings.

High grain yield under moisture stress has generally been associated with high kernel weight. For example, Kimurto (personal communications) attributed high grain yield of Chozi and Duma under drought to the high kernel weight and seeds per head. Guttieri *et al.* (2001), from a study carried to evaluate the stability of grain yield and its components under moisture stress condition, found increased kernel size as a result of reduced tiller number plant. Similar results have been reported in other crops (Omanya *et al.*, 1996). It is not quite clear why, in this study, the drought tolerant varieties (except Chozi) did not have higher TKW than drought sensitive varieties at low moisture level as expected. This result is quite baffling considering that drought tolerant varieties had lower number of tillers, and lower number of seed per spike but yet gave greater grain yield than the drought susceptible ones at low moisture level.

Drought tolerant cultivars recorded lower seed number per spike than the drought sensitive. The low seed number per spike could probably be due to the low number of tillers per plant as consistently shown by the drought tolerant cultivars. This contradicts earlier findings by Simane *et al.* (1993) that more tillers per plant result into fewer seeds per spike. However, the low number of seeds per spike of drought tolerant varieties did not lead to higher TKW as is expected. A decrease in spike number and/or kernel number per spike, causes an increase in kernel weight (Keim and Kronstad, 1981).

We can therefore conclude that yield components have a great role in modifying the plants for specific environmental conditions. Wheat varieties meant for moisture stress environments may be those with fewer tillers that will help avoid wasteful non-productive tillers that will require additional nutrients and moisture. However, such

plants may need to have shorter plant stature to help reduce the unnecessary load that may require extra nutrients and moisture. The plant height as a component for plant survival under low moisture should, nevertheless, not compromise pre-anthesis biomass accumulation that is necessary for high yields.

5.3. Genotypic Correlation for agronomic characters affecting grain yield and water use efficiency (WUE) of wheat under two moisture levels

Biomass had a significant positive effect on WUE under both low and high moisture regimes. Partitioning of this positive effect of biomass on WUE, through path coefficient analysis, revealed that biomass had both direct effect and indirect effect (via plant height and seed number per spike) on WUE of drought tolerant varieties under low moisture condition. On average, the direct effect component accounted for 17% while indirect effect (via plant height and seed number per spike) accounted for 83% of the variation. Thus biomass appears to be an important trait that could be used in selecting for high WUE, especially under low moisture environments. This could be done by indirectly selecting for shorter plants that have a higher seed number per spike.

Number of tillers per plant had a positive (low moisture) and negative (high moisture) correlation with WUE of Duma. Furthermore, path coefficient analysis revealed a strong positive effect of tillers per plant on WUE of Duma, Ngamia and Chozi under low moisture. The results of this study imply that tillering ability may be used as a selection criterion for high WUE under moisture stress conditions. These results are in agreement with earlier findings (e.g., Common and Klink, 1981; Simane *et al.*, 1993) that genotypes having limited number of tillers, i.e., two or three tillers will do better under water-limited conditions. Also, Islam and Sedgley (1981) and Dofing and Karlsson (1993)

advocated 'uniculm ideotypes' for water-limited environments. However, Hadji-christdoulou (1985) advocated profuse tillering capacity for varieties adapted to moisture stress environments.

Grain yield was positively correlated to most of the traits studied under both moisture regimes. Under low moisture condition, grain yield had greater positive relationship with HI, biomass, plant height and seed number per spike for nearly all the cultivars tested but the effect was greater for drought tolerant varieties than the drought susceptible ones. Therefore biomass and HI may form part of the target traits for selection for drought tolerance in wheat. However, in semi-arid or water-limited conditions, where the rainfall distribution is highly variable from season to season, the potential yield under stress may not be the best indicator for drought resistance (Simane *et al.*, 1993b).

5.4. Path effects on water use efficiency of six wheat genotypes

Water stress is the most important limitation to wheat productivity in water -limited environments of the world. Therefore, the development of wheat cultivars that use available water more efficiently and that are tolerant drought is a major goal for increasing productivity in drought prone environments. Water use efficiency is considered an important component of adaptation to drought (Ehdaie and Waines, 1993). Besides, genetic variation for plant WUE exists both among and within species (Briggs and Shantz, 1914). These variations in adaptation are due to many factors among them yield components. The contributions of different yield components to variation in the WUE of six wheat genotypes are discussed below.

5.4.1. Path effects of tillers per plant on water use efficiency

Path coefficient analysis showed low (drought susceptible cultivars with the exception of Pasa) to strong (drought tolerant cultivars) positive overall effect of number tillers per plant on WUE under low moisture condition. The strong positive effect of tiller number per plant on WUE of drought tolerant varieties was due to the strong direct path effect. For the drought susceptible varieties, however, the strong direct path effect was partially counterbalanced by the indirect negative effects via plant height, biomass and seeds per spike. Overall, tiller number per plant accounted for about 50% of the variation in WUE of the test cultivars. This suggests that tiller number per plant may be a good indicator of WUE under moisture stress and may thus be of considerable importance in selecting for high WUE in dry environments. These results are in line with earlier findings by Ehlig and Le Mert (1976) and Cone *et al.* (1995).

5.4.2. Path effects of plant height on water use efficiency

Generally plant height had negative effect on the water use efficiency of all the cultivars (except for Ngamia and Mbuni) at low moisture level. Moreover, path coefficient analysis revealed that both the direct and indirect effects of plant height on WUE were very low under low moisture regime. This implies that although short plant height may lead to greater WUE in dry environments, plant height alone may not be a very effective criterion for selecting for high WUE in dry environments. Rather, selecting shorter plants with increased pre-anthesis biomass accumulation (Turner and Nicolas, 1987; Wahbi and Gregory, 1990) may be more useful.

5.4.3. Path effects of biomass on water use efficiency

The effect of biomass on WUE was generally high and positive for drought tolerant cultivars but negative for drought susceptible ones at low moisture level. However, the direct path effect was much lower than the indirect effects via (plant height and seed number per plant). This suggests that rather than direct selection for biomass, indirect selection for plant height and seed number per spike may be more important to achieving greater WUE in a breeding program. This does not contradict earlier findings by Richards *et al.*, (1999) that reducing plant height may lead to yield improvement by improving HI.

5.4.4. Path effects of seeds per spike on water use efficiency

The direct effect of seed number per spike on WUE, on average, was negative and weak at low both low and high moisture regimes. This low negative effect was most likely due to the wide variation (with genotypes) of the direct and indirect effects, both in sign and magnitude. For example, at low moisture level the direct effect of seed number per spike varied from -0.004 (Mbuni) to 0.485 (Pasa) and there was no distinct pattern to this variation. Such a low impact of direct effects implies that direct selection for seed number per spike would not be effective for improving WUE in wheat in both marginal and high rainfall areas. This finding is not in agreement with those reported by Mayoral and Atsmon (1982).

5.5. Path effects on grain yield of six wheat genotypes

Any genetic advancement in yield in a dry environment should have an interactive effect of yield components. The most likely traits to improve yields in a given environment can be identified if the understanding of the agronomic traits is adequate. The use of agronomic traits in a breeding program, either by direct selection or through traits associated with yield, can then result in more precise targeting of factors limiting yield and may result in faster rates of yield improvement (Richards *et al.*, 1999). In this study, yield was considered to be the complex outcome of different agronomic characters (namely tillers per plant, plant height, biomass and seed number per spike). Consequently, the direct and indirect effects of these characters on yield were analyzed and are discussed below.

5.5.1. Path effects of number of tillers per plant on grain yield

Number of tillers per plant had low (low moisture) to very low direct (high moisture) effect on grain yield. The low path effect of tillers per plant on grain yield at low moisture could be due to the fact that two of the test varieties (Chozi and Mbuni) had moderately strong negative path effects while the rest had positive path effects. It is not quite clear as to why there was variation in the sign of path effects in this case. These results suggest that direct selection for tiller number per plant would not be effective for improving grain yield in wheat in both marginal and high rainfall environments. These results contradict agreement earlier findings (Rebetzke *et al.*, 2001; Cone *et al.*, 1995).

5.5.2. Path effects of plant height on grain yield

The path effect of plant height on grain yield was positive but low (high moisture) to very low (low moisture). This unexpectedly low direct effect of plant height at low moisture level could be due to the fact that the drought tolerant varieties had moderately strong positive path effect while the susceptible ones had negative effects. Thus the negative effect of the susceptible varieties almost cancelled the positive effects of the tolerant varieties. These results do not contradict earlier findings (Blum and Sullivan, 1997) that shorter plants have been associated with drought tolerance in wheat. However, results from the current study imply that direct selection for plant height may not be effective in improving grain yield in wheat.

5.5.3 Path effects of biomass on grain yield

Path analysis of grain yield and agronomic characters demonstrated that biomass exerted the largest influence both directly and indirectly upon grain yield at low moisture level. This is consistent with the results of correlation analysis, which revealed that biomass had the strongest correlation with grain yield at low moisture level. At high moisture, in contrast, the direct and indirect effect of biomass upon grain yield was negative and very low and this could be attributed to the large variation in both the magnitude and sign of these effects. For example, the direct effect of biomass on grain yield was moderately high and negative for drought tolerant varieties but positive for drought susceptible varieties. This suggests that at high moisture the drought tolerant varieties would not be able to convert high biomass yield into greater grain yield. Thus, higher biomass would lead to higher HI (for drought tolerant varieties) only under water stress conditions.

Passioura (1977) has also reported that grain yield in water-limited environments is the product of crop use, WUE and HI.

5.5.4. Path effects of seeds per spike on grain yield

Both the direct (positive) and indirect (negative) effect of seeds per spike on grain yield was very weak under low moisture condition but moderately strong and positive under high moisture regime. The very weak effect of seeds per spike on grain yield at low moisture level could have been due to the variation in the magnitude and sign of both the direct and indirect effects. For example, all varieties (except Chozi and Mbuni) had positive direct effect as expected. It is not quite clear why Chozi (drought tolerant) and Mbuni (drought susceptible) gave contrasting results to the other varieties. Earlier studies have shown that seeds per spike have stable indirect effects via plant height and biomass in moisture stress environments (Simane *et al.*, 1993).

6.0. CONCLUSION AND RECOMMENDATION

This study assessed the genotypic variation in water use efficiency and grain yield and the correlation between WUE and various agronomic traits among six wheat genotypes grown under low and high moisture regimes. The main conclusions of this study are:

1. Drought tolerant cultivars were more efficient in moisture utilization especially under low moisture condition.
2. The high water use efficiency was attributed mainly to high harvesting index and biomass.

3. There were both direct and indirect effects of agronomic traits upon grain yield and water use efficiency.
4. At low moisture level, the effect of tillers per plant on WUE was low and positive for the drought tolerant cultivars tested.
5. At low moisture level, plant height had a negative overall path effect on the WUE of drought susceptible cultivars.
6. Biomass and seeds per spike had positive path effect on WUE at low moisture level.
7. At low moisture level, path effects of tillers per plant on grain yield was positive for all the cultivars tested (except for Chози).

The hypothesis tested was that there is genetic variation in WUE of selected wheat genotypes and that there are both direct and indirect effects of agronomic traits on WUE of these genotypes. The hypothesis has not been disapproved. Although no significant effects of cultivar on WUE were detected, drought tolerant varieties had higher WUE values than the drought sensitive ones at low moisture level while the converse was true at high moisture level. In addition, path analysis revealed that there were both direct and indirect effects of agronomic traits on WUE but these effects varied greatly in magnitude and sign.

To fully understand the direct and indirect effects of agronomic traits on WUE and grain yield in wheat, further research is recommended. This should entail evaluation of the existing commercial wheat cultivars to identify useful traits that lead to improved WUE and grain yield in moisture stress environments. It is important to undertake this direction of research because the traits influencing early vigour such as a large embryo

size, a high specific leaf area and the appearance of a coleoptile tiller, which are often absent in most of spring wheats, are being incorporated in current wheats.

7.0 REFERENCES

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