GROWTH, BIOMASS PARTITIONING AND PHYSIOLOGICAL RESPONSES OF THREE CHICKPEA (*CICER ARIETINUM* L.) ACCESSIONS SUBJECTED TO MOISTURE STRESS AT TWO PHOSPHORUS LEVELS

A THESIS SUMITTED TO THE SCHOOL OF GRADUATE STUDIES IN PARTIAL FULLFILMENT OF THE REQUIRMENTS FOR THE DEGREE OF MASTER OF SCIENCE IN BIOLOGY

BY

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2007

ADDIS ABABA UNIVERSITY

SCHOOL OF GRADUATE STUDIES

DEPARTMENT OF BIOLOGY

Growth, biomass partitioning, and physiological responses of three chickpea (*Cicer arietinum** *L) accessions subjected to moisture stress at two phosphorus levels

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ACKNOWLEDGEMENTS

I am deeply grateful to my advisors; Prof. Masresha Fetene and Dr. Taddesse W/mariam for their excellent guidance, cooperation, frequent advice and follow-up of this work.

I would also like to extend my heartfelt gratitude to Solomon Zewdie; a Ph.D student, for his unreserved help and support in clearing blurred images and providing valuable suggestions, starting from the beginning of the study. I also appreciate the cooperation provided by the Ecophysiology laboratory staff members.

I am thankful to my wife Aynadis Anagaw for her encouragement and patience that she showed throughout my study.

I express my gratitude to the Department of Biology, Addis Ababa University for sponsoring the study and to the Institute of Biodiversity Conservation and Research (IBCR) for providing the seeds of chickpea accessions and to all others who contributed in some way to the completion of this work.

TABLE OF CONTENTS

Page

LIST OF FIGURES

LIST OF TABLES

Abstract

Water deficit and Phosphorus stresses are important limiting factors in agricultural production. The effects of moisture stress and phosphorus deficiency on growth, physiology, yield and yield components of three chickpea (*Cicer arietinum L*) accessions; Yaya Gulele, Legambo and Moretna Jiru were investigated under greenhouse condition. The study was conducted by inducing moisture stress at the vegetative; 28 days after planting (DAP) and flowering; 52 days after planting (DAP) stages of chickpea plants under two phosphorus (low and normal) levels.

A general decrease in growth parameters was observed in almost all moisture stressed and phosphorus deficient chickpea plants of all accessions, which was mainly through lower total leaf area that further decreased light interception. In contrast, root relative growth rate (RGR) and dry weight were higher for phosphorus deficient plants except for plants of accession Moretna Jiru. For drought induced at vegetative stage, chickpea plants of accession Yaya Gulele grown under normal phosphorus-low water stress (NP-LWS) had the highest plant height and total leaf area. Moreover, plants of this accession treated with normal phosphorus-moderate water stress (NP-MWS) had the highest relative growth rate (RGR) as compared to plants of other accessions. The highest number of leaf/plant was recorded in plants of accession Moretna Jiru treated with NP-LWS. Similarly, plants of accessions Legambo and Moretna Jiru grown under NP-LWS had the highest leaf and stem dry weight.

In addition, chickpea plants of accessions Yaya Gulele and Moretna Jiru were able to maintain relatively higher midday relative water content (RWC) mainly under normal phosphorus treatments than plants of accession Legambo, both for moisture stress induced at vegetative and flowering stages. This probably helped plants of these accessions to have a better photosynthetic performance that can be expressed by higher maximal quantum yield (Fv/Fm) and effective quantum yield (ΔF/Fm’) of PS II.

Yield and yield components were reduced by drought and phosphorus deficiency both for drought imposed at vegetative and flowering stages. Statistically significant differences in yield and yield components were not observed among accessions across the various treatments for drought induced at vegetative stage. However, for drought induced at flowering stage, chickpea plants of accession Legambo grown under NP-LWS, NP-MWS and low phosphorus-low water stress (LP-LWS) had greater numbers of pods than plants of accession Moretna Jiru. Similarly, plants of accession Legambo treated with LP-LWS had greater numbers of pods than plants of accession Yaya Gulele. Plants of accession Yaya Gulele had higher pod weight than plants of accession Moretna Jiru under the various treatments. Moreover, plants of accession Yaya Gulele treated with NP-LWS and LP-LWS had higher seed weight than plants of accessions Legambo and Moretna Jiru, respectively. Generally, better root growth, leaf relative water content (RWC) and photosynthetic performance in chickpea plants of accession Yaya Gulele, early flowering and better root growth in plants of accession Legambo and lower total leaf area, leaf relative water content (RWC) and better photosynthetic performance in chickpea plants of accession Moretna Jiru were found to be adaptive mechanisms to drought and phosphorus deficiency.

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1. INTRODUCTION

In the natural environment, plants are subjected to several stress factors that adversely influence growth, metabolism and yield. Stress is any significant deviation in environmental factors from the conditions optimal for normal functioning of plants (Salisbury and Ross, 1992). Stress may be caused either by biotic (insects, bacteria, fungi and viruses) or abiotic (water availability, nutrient, light, temperature e.t.c.) factors. Among these, moisture stress is the major abiotic factor that determines the kinds and amounts of natural vegetation as well as agricultural crop production all over the world in general and in the sub-Saharan regions in particular (Farah et al., 1988; Chaves et al., 2000; and Germ et al., 2005). This is because the lack of adequate soil moisture in the seedbed is an important constraint responsible for poor plant stand due to non-germination of viable seeds, with a consequent reduction in yield. Rains during and after seed germination contribute not only to adequate soil moisture reserves but also are important in establishing uniform and vigorous plant stands (Saxena, 1987; Calcagno and Gallo, 1993 and Siddique et al., 1999).

Phosphorus is an important plant macronutrient, making up about 0.2% of a plant's dry weight. It is a component of key molecules such as nucleic acids, phospholipids, ATP and also involved in controlling key enzyme reactions and in the regulation of metabolic pathways (Schachtman et al., 1998). Although the total amount of phosphorus in the soil may be high, it is often present in unavailable forms or in forms that are only available outside of the rhizosphere. Therefore, the deficiency could be caused either by the low availability of the nutrient in question or due to immobilization. Under such circumstances, different species of plants respond differently. This differential response could be due to variations in plant nutrient requirements, root system morphology and physiology. Moreover, some plants are also able to obtain nutrients like N_2 by symbiosis and P by mycorrhizal associations, where an extensive network of hyphae extends from the root, enabling the plant to explore a greater volume of soil, thereby overcoming limitations imposed by the slow diffusion of Pi in the soil (Schachtman et al., 1998 and Salisbury and Ross, 1992). Many soils in tropical regions are deficient in one or more of the mineral nutrients essential for plant growth and there is a general agreement that nitrogen and phosphorus are two plant nutrients most often deficient in the tropics (Singh and Das, 1987 and Koala et al., 1988). Similarly, soils of the highlands of Ethiopia are known to be poor in nitrogen and phosphorus (Tekalign Mamo et al., 1988 and Sahlemedhin Sertsu, 1988 cited in Masresha Fetene and Amha Belay, 1988). However, all cultivated legumes possess the ability to reduce atmospheric dinitrogen (N_2) symbiotically to satisfy their needs. Therefore, restrictions on plant growth are caused by scarcity of other resources such as phosphorus, which is strongly bound in soil, resulting in a low rate of diffusion towards the root surface (Jensen et al., 2002). Moreover, of all nutrients, shortage of phosphorus has the biggest impact on legumes, which generally rely on nitrogen fixation for nitrogen nutrition. The deficiency of this nutrient often limits nitrogen fixation through its effect on growth and survival of rhizobia, nodule formation, nodule functioning and host plant growth (Tang et al., 2001).

In Ethiopia, chickpea (*Cicer arietinum L.*) is a valuable source of food especially for the lower income sectors of the population, and is used as soil fertility restorer and also has an economic value (Asfaw Telaye, 1988). Chickpea is grown in poorly drained and phosphorus deficient vertisols in the highland regions mainly in Wello, Tigray, Gojjam, Gonder and Shewa provinces of the country. It is cultivated as a rainfed crop on residual moisture, where its yield is mostly affected by terminal drought (Tamirie Hawando, 1987 and Asfaw Telaye et al., 1994). It is generally believed that moisture stress (drought) accounts for nearly 20-50% of the variation in chickpea production caused by both biotic and abiotic stress factors (Saxena, 1987 and Saxena et al., 1993). However, the potential to increase average chickpea yield in Ethiopia is promising by selecting improved, high-yielding chickpea genotypes that are tolerant to soil and climatic stresses. This research aims at adding information to the already accumulated knowledge and helps to identify growth, biomass partitioning and physiological responses of chickpea accessions to drought and phosphorus deficiency.

1.1. Objectives of the study

General objectives

- To investigate growth, water relation, photosynthesis and the consequent yield responses of three chickpea accessions to a combination of moisture and phosphorus stresses.

Specific objectives

- To evaluate the effect of moisture and phosphorus stresses on the growth and biomass partitioning patterns in three chickpea accessions.
- To explain and compare physiological changes made by the three accessions in response to drought and phosphorus deficiency.
- To see how fine root biomass responds to drought and phosphorus deficiency.
- To identify morphological and/or physiological traits associated with drought tolerance and also better yield under moisture and phosphorus stresses.

2. LITERATURE REVIEW

2.1. Botany and agroecology of chickpea

Chickpea (*Cicer arietinum* L.) is a self-pollinating, annual, cool season grain legume. It belongs to the family *Leguminosae*, tribe *Ciceraea* and genus *Cicer*. Two types of chickpea are recognized; Desi (colored, small seeded, angular and fibrous) type which is grown in the semi arid tropics and Kabuli (beige, large seeded, rams head shaped with lower fiber content) type that is grown in temperate regions (Muehlbauer and Abebe Tullu, 1997 and Asfaw Telaye et al., 1994).

Chickpea is a major food legume in many countries including Algeria, Ethiopia, India, Iran, Mexico, Morocco, Myanmar, Pakistan, Spain, Syria, Tanzania, Tunisia, and Turkey. It is cultivated on 11.33 million hectares in the world with 8.80 million tones produced (Upadhyaya et al., 2001 and FAO, 2004). Of the world production, 91% is produced in Asia, 3.0% in Africa, 1.0% in Europe, 2.5% in North and Central America (mainly Mexico), and 2.4% in Oceania (mainly Australia). In Asia, India accounts for 70.6% of the area and 74.8% of the production. Other important Asian countries such as Iran, Myanmar, Pakistan, and Turkey account for 26.9% of the area and 22.6% of the production (Upadhyaya et al., 2001). The major chickpea growing areas are in the arid and semi-arid zones. About 90% of the world’s chickpea is grown under rain fed conditions, where terminal drought is one of the major constraints limiting productivity (Kashiwagi et al., 2006). Thus, the average world productivity of 0.78 t/ha is low (Upadhyaya et al., 2001).

In Ethiopia, chickpea is the third most important pulse crop next to faba bean and field pea. It is grown in areas with annual rainfall ranging between 950-1800 mm and altitudes ranging between 1400-2300 above sea level (Tamirie Hawando, 1987; Million Eshete and Benewal, S. P.S, 1988). In terms of major agroecological zones, the major chickpea producing areas follow the pattern of rainfall distribution in the country and roughly lie between 9^0 and 16^0 longitudes (Asfaw Telaye et al., 1994). Under Ethiopian conditions, chickpea is grown mostly under a few rainshowers during the first part of its vegetative development stage with the rest of the crop growth depending completely on residual moisture. The success of this crop thus, depends upon the rains received from mid June to mid October (Tamirie Hawando, 1987; Asfaw Telaye, 1988 and Asfaw Telaye et al., 1994). Chickpea is grown mostly in poorly drained and water logged soil in the highland regions. The available phosphorus in this soil is low to very low and hence chickpea responds well to phosphorus fertilization (Tamirie Hawando, 1987 and Tekalign Mamo, 1988).

Chickpea (*Cicer arietinum* L.) originate from the Southeastern part of the present day Turkey adjoining Syria. This is based on the presence of closely related wild species, *Cicer reticulatum* Lad. Zinsky and *C.echinospermum* P.H. Davis (Muehlbauer and Abebe Tullu, 1997). Wild *C. reticulatum* is closely related to the cultivated *Cicer arietinum* and thus, is regarded as the wild progenitor of chickpea. Botanical and archeological evidences show that chickpeas were first domesticated in the Middle East and were widely cultivated in India, Mediterranean area, the Middle East and Ethiopia (Purseglove, 1974b; Hailu Mekbib et al., 1991; Asfaw Telaye et al., 1994 and Muehlbauer and Abebe Tullu, 1997). Nowadays, Ethiopia is considered as the secondary center of diversity consisting, a total of 859 accessions, composed of 162 selections, 4 donated accessions and 693 Plant Genetic Resource Center/Ethiopia collections (Dawit Taddesse et al., 1994). All the accessions are found conserved in the gene bank located at the Institute of Biodiversity Conservation and Research (IBCR).

In Ethiopia, chickpea seeds are consumed in one form or another as a protein supplement in everyday meals of both the urban and rural people. In the traditional food preparation, the matured seeds of chickpea are eaten either boiled (*nifro*), dehulled split (*kik*) or whole roasted *(kollo*) (Senayit Yetneberk and Asrat Wondimu, 1994). Moreover, traditionally chickpea is used as a medicinal plant, because glandular secretions of the leaves, stems and pods consist of malic and oxalic acids. In India, these acids are harvested by spreading thin muslin over the crop during the night. In the morning the soaked cloth is wrung out and the acids are collected in bottles. Then, it is used to treat diseases such as bronchitis, cholera, constipation, diarrhea and snakebite. The acids are also supposed to lower the blood cholesterol levels (Muehlbauer and Abebe Tullu, 1997).

Ethiopia ranks fourth in world chickpea production and land allocation (FAO, 1977-1984; cited in Asfaw Telaye, 1988). Nevertheless, the contribution of Ethiopia to the world is only 1.5% and 1.6%, respectively (Asfaw Telaye, 1988). However, Ethiopia ranks third in Africa in terms of yield (700-1100 kg/ha) next to Egypt (1800-2000 kg/ha) and Sudan (1000-1100 kg/ha), contributing 45% of the production (Tamirie Hawando, 1987 and Asfaw Telaye, 1988).

The productivity of chickpea has remained fairly static at 0.78 t/ha for several years. This is because of the susceptibility of chickpea accessions to biotic (diseases, pests, weeds e.t.c.) and abiotic (drought, water logging, nutrient deficiency e.t.c.) stresses due to the narrow genetic diversity of the accessions (Tamirie Hawando, 1987; Brown et al., 1989 and Nayyar et al., 2005). Terminal drought is the major constraint for the large yield reduction in chickpea when it mainly occurs during late vegetative and reproductive stages (Saxena et al., 1993 and Ashley, 1999) and it is generally believed that drought accounts for nearly 20 to 50% of the variation in chickpea production caused by both biotic and abiotic stress factors (Saxena, 1987 and Saxena et al., 1993).

2.2. Effects of drought and phosphorus deficiency on plant growth and physiology

Plants respond to drought through modification of their morphological, physiological and metabolic processes. These responses are complex processes involving deleterious and/or adaptive changes. Under field conditions, such responses can be synergistically or antagonistically modified by the superimposition of other stresses (Chaves et al., 2002) such as phosphorus deficiency. Early responses to drought and phosphorus deficiency aid immediate survival of the plant, whereas acclimation, calling on new metabolic and structural capabilities mediated by altered gene expression, helps to improve plant functioning under stress.

2.2.1. Effects of drought and phosphorus deficiency on plant growth

Actively growing components of plants are characterized by active cell division, enlargement and differentiation, each of which requires different amount of water. The occurrence of drought at this stage adversely affects growth (Fitter and Hay, 1987; Chaves et al., 2002 and Liu et al., 2004). This is because, in addition to decreasing the turgor pressure inside actively dividing cells, drought decreases photosynthetic rate in plants and disrupts carbohydrate metabolism in leaves, nitrogen fixation in the roots; all may lead to reduced amount of assimilate available for export to actively growing plant organs including reproductive organs (Hooda et al., 1989 and Liu et al., 2004). Furthermore, frequent soil drying during drought is likely to induce a decrease in nutrient availability, particularly phosphorus due to its reduced diffusion ability and poor uptake by the roots. This will have a strong interactive effect on plant growth and function (Koala et al., 1988; Marschner, 1995 and Singh et al., 2006). A low phosphorus status together with drought induce changes in the relative growth of roots, nodules and shoots rather than changes in nitrogen and/or carbon uptake rates per unit mass or areas of these organs (Hooda et al., 1989 and Jensen et al., 2002).

Some of the responses to drought and phosphorus deficiency occur at the leaf level in response to stimuli generated in the leaf itself or somewhere in the plant. Leaf area and plant height development are important factors in crop production, as leaf area affects the amount of radiation intercepted and carbon assimilated. At the same time plant height determines the number of nodes and the consequent fruiting branches, which increase with increasing plant height (Yemane Asgidom and Skjelvag, 2003 and Singh et al., 2006). These growth parameters are very sensitive to drought and phosphorus deficiency (Nielsen and Nelson, 1998 and Singh et al., 2006) and phosphorus deficiency severely inhibits leaf growth rate by inhibiting cell expansion, which is directly related to the amount of available water to the root cells. This is due to the fact that phosphorus deficiency results in low hydraulic conductance of the root system (Rao and Terry, 1989). Reduced number of leaves in dicots is also due to lower number of nodes for branching that is in turn related to plant height (Marschner, 1995 and Singh et al., 2006). Therefore, water stress and phosphorus deficiency reduce plant height, number of leaves through their effect on node initiation, leaf area, CO_2 acquisition for the plant as a whole due to a decline in total leaf area, leaf area per unit weight and utilization of incoming light and biomass production (Hooda et al., 1989 and Jensen et al., 2002).

Drought and phosphorus deficiency mostly reduce shoot growth and increase relatively dry matter partition into the root, leading to an increasing root/shoot ratio (Fitter and Hay, 1987; Gregory, 1988; Jensen et al., 2002 and Kage et al., 2004). This is because water and nutrient uptake may be limited by the amount of roots in a particular soil layer and hence root growth is favored compared with shoot growth under conditions of drought and phosphorus deficiency. Moreover, root respiration and nitrogen fixation per unit root mass are lower and the assimilates partitioned to the root system are used mainly to increase the size of the root system so as to have deep, prolific and enhanced root growth that can reduce drought and nutrient stress (Gregory, 1988; Jensen et al., 2002; Kage et al., 2004 and Serraj et al., 2004). In chickpea, root mass and total length are slightly reduced under low phosphorus supply. But morphological changes such as increased branching density occur, which again insure a greater root surface contact with the soil (Alloush, 2003). The very important components of roots that function primarily as resource-capture organs, where their responses comprise a major component of the whole plant response to changes in soil environment are the fine roots (Pregitzer, 2002). They range in size between 0.5 mm to 2 mm in diameter and account for a significant portion of the total net primary productivity (Vogt and Persson, 1991 and Pregitzer, 2002). According to the source-sink theory of resource allocation, trees growing on infertile sites should allocate a greater proportion of their resources into fine root production than those growing on fertile sites, as this investment in nutrient acquisition should increase growth and/or reproduction (Maycock and Condon, 2000). Fine root biomass in soils with low available phosphorus is greater and lower in soils with high available phosphorus. In general, fine root biomass is positively correlated to available moisture in the soil and negatively to the available nutrient (Maycock and Condon, 2000 and Ostertag, 2001).

Symbiotic nitrogen fixation is highly sensitive to drought and nutrient deficiency, particularly to phosphorus. Drought and phosphorus deficiency reduce plant growth and hence N-demand and N_2 fixation. The effect of these stress factors on nodule biomass is the same as the effect on the host plant growth, i.e. inhibit growth by restricting assimilate supply from the host plant (Koala et al., 1988; Tang et al., 2001 and Jensen et al., 2002). But evidences concerning the regulatory mechanisms are conflicting. Some forwarded the regulation as taking place in the photosynthetic apparatus, thereby affecting the production and supply of non-structural carbohydrates to the nodules. Others suggested as a direct effect on nitrogenase activity in the nodules (Gregory, 1988 and Jensen et al., 2002). Thus, decreased plant nitrogen status may affect protein synthesis, including the key enzymes for carbon assimilation and metabolism, which in turn would affect plant carbohydrate status (Liu et al., 2004).

2.2.2. Effects of drought and phosphorus deficiency on plant physiology

Plant metabolism is dependent on leaf water status, which can be measured by leaf relative water content (RWC) and leaf water potential (LWP). The photosynthetic rates of leaves of C_3 and C_4 plants decrease as their leaf relative water content and water potential decrease (Lawlor, 2002). This decrease is attributed to reduced stomatal conductance, which restricts the supply of CO_2 to metabolism (stomatal limitation) and metabolic impairment i.e. non-stomatal limitation (Teulat et al., 1997; Lawlor, 2002 and Cornic and Fresneau, 2002). Under field conditions, when water deficit develops slowly, one of the first events to take place in plants is presumably stomatal closure in response to the migration of chemical compounds synthesized in dehydrating roots (Chaves et al., 2002 and Flexas and Medrano, 2002). Stomatal closure restricts CO_2 entry into the leaves thereby decreasing CO_2 assimilation and water loss from the leaves (Parry et al., 2002; Lawlor, 2002; Chaves et al., 2002; Flexas and Medrano, 2002 and Tilahun Amede and Schubert, 2003). Limited CO_2 assimilation in turn decreases the consumption of electrons released from water as a consequence of the light reaction (Lawlor, 2002 and Herting and Fock, 2002). In addition, Bjorkman and Powles (1984) pointed out that stomatal closure results in elevated temperature of the leaf exposed to high radiation and water deficit stress that would cause heat damage to the photosynthetic system. Non-photochemical quenching by xanthophyll cycle in the photosystem antennae then dissipates the resulting excess excitation energy. In general, under severe and prolonged drought conditions, there is evidence that the decrease in CO_2 assimilation rates in drought stressed leaves cannot be simply reversed by increasing the external CO_2 supply, showing that drought stress must also affect mesophyll metabolism (Lawlor, 2002).

As leaf relative water content (RWC) declines, the relative limitation of CO_2 assimilation by stomatal closure decreases and metabolic limitation increases. The cause of decreased photosynthetic rate at low RWC is therefore limitation of RUBP (ribulose bisphosphate) synthesis, which is again caused by inhibition of ATP (adenosine triphosphate) synthesis due to progressive inactivation or loss of ATP synthase (coupling factor) resulting from ionic concentration, particularly Mg^{2+} as a result of fall in RWC (Lawlor, 2002; Flexas and Medrano, 2002 and Parry et al., 2002). This is because the rate of photosynthesis is dependent on the synthesis of RUBP and activity of Rubisco where its activity is influenced by Rubisco activase. Rubisco activase is an abundant protein that regulates the active site conformation of Rubisco and removes inhibitors, allowing rapid carboxylation. This reaction requires ATP, so decreased activity and activation state of Rubisco at low RWC may be related to inadequate ATP concentration (Parry et al., 2002). In addition, in plants experiencing drought leaf starch and sucrose concentration decreased rapidly and become close to zero, while the concentration of glucose and fructose increased significantly. In the meantime, the resulting high concentration of hexose may be involved either in the feedback regulation of photosynthesis or turgor maintenance, i.e. osmotic adjustment (Chaves et al., 2002; Tilahun Amede and Schubert, 2003 and Liu et al., 2004). Similarly the amount of proteins decrease due to repressed synthesis and increased turnover as a result of decreased ATP synthesis (Lawlor, 2002).

2.2.3. Effects of drought and phosphorus deficiency on yield and yield components

The productivity of crops under drought stress is strongly related to the processes of dry matter partitioning in the plant. An optimal partitioning of dry matter between root and shoot and the further separation of aboveground dry matter between the vegetative and generative organs has a crucial importance for crop yield under drought (Kage et al., 2004). The occurrence of drought and phosphorus deficiency during the development of reproductive structures accentuates the decline in nitrogen fixation and photosynthesis resulting in a further decline in supply of carbon and nitrogen to the pods. The plant is thus unable to meet the nutritional requirements of developing fruits. This leads to an enhanced shedding of premature reproductive structures and senescence and abscission of leaves (Hooda et al., 1989; Liu et al., 2004 and Nayyar et al., 2005). In order to avoid such effects, some annuals exhibit phenological drought avoidance, whereby flowering and seed production occur before water supplies are exhausted. Others resist drought spells by accumulating reserves in different plant parts, normally stems and roots prior to drought. The resources are then remobilized during the reproductive phase (Saxena et al., 1993; Ashley, 1999 and Chaves et al., 2002).

Generally, plants subjected to drought and phosphorus deficiency undergo changes in plant morphology (phenotypic plasticity), which eventually results in a proportional change in physiological processes. Some of the changes include; 1) reducing leaf area for water conservation and carbon acquisition, 2) reducing nodule mass for nitrogen acquisition, and 3) increasing partitioning to the roots for phosphorus and water acquisition (Gregory, 198; Hooda et al., 1989 and Jensen et al., 2002).

Several methods have been developed in the screening of plant species and/or genotypes with respect to stress tolerance. Chlorophyll fluorescence, relative water content and grain yield are some of the most important tools. Among these, chlorophyll fluorescence is very useful to study the effects of environmental stresses on plants since photosynthesis is often reduced in plants experiencing adverse conditions, such as water deficit, temperature, and nutrient deficiency, polluting agents and attack by pathogens. Chlorophyll a fluorescence measurements have the advantages of being non-intrusive, non-destructive and quick (Quiles, 2005). Chlorophyll fluorescence signals can provide valuable and direct information on the extent of stress induced-reduction in the overall efficiency of energy conversion and in the efficiency of PS II photochemistry (Bjorkman and Demmig, 1987 and Laisk et al., 1997). It is now well established that any reduction in the potential quantum yield of PS II (expressed as Fv/Fm) in dark-adapted leaves is a strong quantitative indicator of the reduction in the efficiency of the primary photochemistry of PS II. This is so irrespective of whether the reduction in the Fv/Fm is caused by an increase in non-radiative (thermal) dissipation or a decrease in photochemistry. This reveals damage of PS II or the development of protective mechanisms, down regulating PS II activity (Demmig and Bjorkman, 1987; Laisk et al., 1997; Ensminger et al., 2000; Graffin et al., 2004 and Souza et al., 2004). The indicator function of chlorophyll fluorescence arises from the fact that fluorescence emission is complementary to alternative pathways of de-excitation, which are primarily photochemistry and heat dissipation (Laisk et al., 1997 and Chaves et al., 2002). Fluorescence parameters that are used to assess the status of plants under stressful conditions include effective quantum yield (Fm’-F/Fm’) which measures the proportion of the light absorbed by chlorophyll associated with PSII that is used in photochemistry (related to achieved efficiency of photochemistry), electron transport rate expressed as yield*PAR*0.5*0.84 and non-photochemical quenching (NPQ), which is the amount of absorbed light lost as heat (heat dissipation), q_p and Fv/Fm, which provide information about the underlying processes that have altered efficiency of PSII photochemistry (Maxwell and Johnson, 2000). Lastly, the practical utility of this tool has been demonstrated for screening photosynthetic performance of sorghum under phosphorus deficiency (Ripley et al., 2004) and cold tolerance of photosynthesis in maize (Frecheboud et al., 1999).

On the other hand, relative water content (RWC) is one of the parameters for assessing the severity of drought (Flexas and Medrano, 2002). Because decreasing RWC of the leaves progressively decreases stomatal conductance, slowing CO_2 assimilation that eventually stops, after which CO_2 is evolved. As RWC declines further, approximately below 36-40%, limitation of CO_2 assimilation by stomatal conductance decreases and metabolic limitation increases (Lawlor, 2002). Besides this, RWC has been proposed as a selection criterion for drought tolerance in many crops where selecting plants for high biomass production under drought requires finding a compromise between maximization of carbon assimilation (with high leaf area and stomatal conductance) and/or minimization of transpiration for maintenance of high relative water content (with low leaf area and stomatal conductance) and in many crops a positive correlation between grain yield and RWC has been observed (Teulat et al., 1997). Stomatal conductance has also been used as a tool for selecting drought resistant varieties through its control on the loss of water and carbon balance in plants (Chaves et al., 2002 and Tilahun Amede and Schubert, 2003).

An adequate knowledge base exists on changes in morphological, anatomical and basic physiological and biochemical processes in response to drought and phosphorus deficiency (Saxena, 1987). However, breeding and selection for enhanced yield stability and/or yield potential under drought stress across crop species has shown small progress and only limited success is evident in a few crops. This is partly due to the quantitative and temporal variability in available soil moisture across years, the low genetic variance in yield under drought and the inherent methodological difficulties in evaluating component traits together with the highly complex genetic basis of drought resistance (Kashiwagi et al., 2006). Therefore, prediction of crop performance and optimization of crop management under limited water supply conditions and phosphorus deficiency consequently requires an accurate description of the biomass partitioning processes and the integration of physiological and biochemical parameters into simple morphological indices (Kage et al., 2004).

3. MATERIALS AND METHODS

3.1. Plant material and growing conditions

The experiment was carried out in a greenhouse at Science Faculty, Addis Ababa University between November and July 2005/2006. During the study period in the greenhouse daily temperature and relative humidity were recorded using thermohygrograph. Thus, the mean maximum and minimum temperatures were 37.05±3.0 and 14.81±1 ^{0}C, respectively and the relative humidity ranged between 86.79±3.7 and 58.36±4.6 %.

Three chickpea (*Cicer arietinum* L.) accessions were selected for use in the greenhouse experiment in this study. Seeds of these accessions, 41007 (Yaya Gulele), 41095 (Legambo) and 41212 (Moretena Jiru) were obtained from the Institute of Biodiversity Conservation and Research (IBCR), Addis Ababa. Hereafter, Yaya Gulele, Legambo and Moretena Jiru will be used instead of accession numbers 41007, 41095 and 41212, respectively. Seeds of accessions Yaya Gulele were collected from Northern Shewa, Yaya Gulele Woreda, a locality 38.6 km away from Melka Tulu Addis road to Melka Turi at an altitude of 2670 m above sea level. Seeds of Moretena Jiru were collected from Northern Shewa, Moretena Jiru Woreda, a locality called Kiro, at an altitude of 2640 m above sea level. Similarly, seeds of accession Legambo were collected from Southern Wello, Legambo Woreda, and a locality called Akesta, where the market source was Borena. The selection of the three accessions was based on the research results and recommendations of previous investigation of Yonas Feleke (1999). According to the results of the study, chickpea plants of accession Yaya Gulele had the highest root biomass, root/shoot ratio and better photosynthetic performance under severe water stress. Plants of Legambo had the lowest total leaf area and the least affected root biomass under severe water stress. In the same way, plants of Moretena Jiru had the highest total leaf area under severe water stress, the highest relative growth rate under well-watered and moderate water stressed conditions.

The seeds were allowed to germinate in a petridish on moist paper for three days under room temperature in the laboratory. Germinated seedlings were then transferred to plastic pots (50 cm wide and 9 cm high), perforated at the bottom and filled with 2.606 kg of a mixture of soil and sand (2:1,v/v) and at a density of one seedling per pot. The pots were then fertilized with 100 ml of Long Ashton complete nutrient solution, prepared as described by Hewitt and Smith (1975b) starting from emergence. Distilled water was used in the preparation of the nutrient solution throughout the experiment.

Table: 1. Macronutrient and micronutrient composition of the Long Ashton complete nutrient solution used to water plants, stock solution and amounts of stock solution used to make a liter of the nutrient medium.

			Stock solution requirement	
Compound	g/l	p.p.m (mg/l)	g/l	ml/l
K_2SO4	0.348	K=156, S= 64	21.75	16
$CaCl_2$ anhyd.	0.444	Ca=160, Cl=284	55.5	8
$MgSO_4.7H_2O$	0.368	Mg= 36, S=48	46.0	8
$Na_2HPO_4.12H_2O$	0.478	Na=62, P=41	29.75	16
NH_4NO_3	0.402	N=141	50.25	8
$MnSO_4.4H_2O$	0.00223	Mn=0.55	2.23	1
$ZnSO_4.7H_2O$	0.00029	Zn=0.065	0.29	1
$CuSO_4.5H_2O$	0.00025	Cu=0.064	0.25	1
H_3BO_3	0.0031	B=0.54	3.10	1
$Na_2MoO_4.2H_2O$	0.00012	Mo=0.048	0.12	1
$CoCl_2.6H_2O$	0.000056	Co=0.012	0.053	1

3.2. Treatment and experimental design

All the pots were irrigated with equal volume (100 ml) of tap water daily so that the pot capacity of the soil was maintained at 70-80% until drought induction. The experiment consisted of two parts that differ in time of drought induction; drought induced at the vegetative stage 28 days after planting (DAP) and drought imposed at the flowering stage 52 days after planting (DAP), after 50% of the plants flowered. Equal amount of Long Ashton complete nutrient solution was given to all treatments for every three days except that phosphorus was excluded from low phosphorus treatments starting from emergence. The two levels of phosphorus were low (0 ml/l) and normal (16 ml/l). The pots were brought to pot capacity before planting by immersing seven pots into water and allowing them to drain overnight. The average weight of the pots plus soil at pot capacity was 3528.57±21.43g and the water stress levels were determined on the basis of the average weight of the pots plus soil weighed after 48 hours from the time the wetted soil at pot capacity was allowed to drain. Accordingly, three levels of water stress were determined as low, moderate and severe, where the soil water content of the pots was maintained at 70%, 40% and 25%, respectively. In general, there were a total of six treatments so as to see the interactive effects of water stress levels and phosphorus. These include:

a) Normal phosphorus-low water stress (NP-LWS).
b) Normal phosphorus-moderate water stress **(**NP-MWS**).**
c) Normal phosphorus-severe water stress **(**NP-SWS).
d) Low phosphorus-low water stress (LP-LWS).
e) Low phosphorus-moderate water stress (LP-MWS).
f) Low phosphorus-severe water stress (LP-SWS).

During the experiment moisture loss was monitored daily by weighing four pots randomly from each treatment and the amount of water lost was replenished. Pots were moved and rearranged occasionally to have a random distribution of growth conditions in the greenhouse.

The experiment was conducted following randomized complete block design with three replications. Each replication consisted of 18 pots (6 pots per accession) and all were used for the determination of various parameters

3.3. Soil analysis

3.3.1. Determination of soil pH

A 1:1 soil water ratio was used according to Juo (1978) to determine soil pH. Twenty grams of soil was mixed with 20 ml of distilled water. The suspension was stirred occasionally and pH was determined after 30 minutes using Digital pH meter (NIG 333, 123, Industrial Estate, Ambala Canntt-133 006) standardized by buffer solution of pH 4 and 7.

3.3.2. Determination of total nitrogen

Total nitrogen of the soil was determined as described in Sahlemedhin Sertsu and Taye Bekele (2000) using macro-kjeldahl method. This method involves three processes: digestion, distillation and titration. During digestion organic nitrogen is converted into ammonium nitrogen with the help of potassium sulphate (K_2SO_4) to raise the temperature and cupric sulphate ($CuSO_4.5H_2O$) as a catalyst.

$$\text{Organic nitrogen} + H_2SO_4 \xrightarrow[CuSO_4.5H_2O]{K_2SO_4} (NH_4)_2SO_4 + H_2O.$$

The amount of nitrogen is then estimated from the amount of ammonia liberated by distilling the digest with alkali (NaOH).

$$2(NH_4)_2SO_4 + 4NaOH \longrightarrow Na_2SO_4 + 4NH_3 + 4H_2O$$

The ammonia liberated is trapped by Boric acid and titrated using HCl.

$$NH_3 + H_3BO_3 \longrightarrow NH_4\,H_2BO_3$$

$NH_4H_2BO_3 + HCl \longrightarrow NH_4Cl + H_3BO_3$

One gram of soil sample, passed through a 0.5 mm sieve and two gram of mixture of potassium sulphate and cupric sulphate were added into the macro-kjeldahl tube. The mixture was moistened with distilled water, shaken and 7 ml of concentrated sulphuric acid (H_2SO_4) was added. The mixture was then digested at 300 ^{0}C in the digestion stand for about three hours until a clear green solution developed. Then 75 ml of 40% sodium hydroxide was added into the digest for distillation. The distillate was received in 20 ml of 2% boric acid mixed indicators and titrated with 0.1N HCl until the green color of the distillate changed to pink. Similarly the blank was passed through all the steps side by side like that of the sample to compensate for any contributions from the reagents used. Lastly, the percent (%) of nitrogen present in the soil sample was calculated as follows:

$$\boxed{\%N = \frac{(a-b)*N*0.014*100}{S}}$$

Where, a = ml of HCl required for titration of the sample.

b = ml of HCl required for titration of the blank.

S =air dried weight of soil sample in grams

N =normality of the titrant (HCl).

3.3.3. Determination of soil available phosphorus

Available phosphorus in the soil was determined following Bray No 1 method as indicated in Juo (1978). This method was selected due to the acidic pH of the soil sample. Two gram of soil sample sieved to 2 mm and 7 ml of extracting solution were added into 15 ml centrifuge tube. This was shaken for a minute and centrifuged for 15 minutes. Then 2ml of the clear supernatant was pipetted into 20 ml test tube where 5ml distilled water and 2ml ammonium molybdate solution were added into it and mixed properly. Hereafter, one ml of diluted stannous chloride ($SnCl_2.2H_2O$) solution was added and the transmittance of the resulting complex was determined after five minutes using Jenway 6405 UV/Vis. Spectrophotometer at 660nm. The concentration of available phosphorus in the soil was calculated from the standard curve obtained with known concentration of phosphorus as follows:

$$\boxed{\textbf{P.p.m of P} = (a-b)*7/S \text{ or } (a-b)*3.5}$$

Where, a = p.p.m P (mg/l P) in sample extract.

b = p.p.m P (mg/l P) in blank.

S = sample weight in grams.

7 = ml of extracting solution.

3.5 = extraction ratio.

3.4. Measurements

3.4.1. Leaf number

The leaf number of three randomly selected plants per treatment was counted and recorded on 28, 42 and 56 DAP.

3.4.2. Plant height

Plant height of three randomly selected plants per treatment was measured and recorded. The measurements were made from the base to the possible highest point of the plant on 28, 42 and 56 DAP.

3.4.3. Total leaf area

The areas of five randomly selected leaflets were determined by an area meter (Delta T devices Ltd., Cambridge, England). Then the method of Adjei-Twum and Splittstorsser (1976) with little modification as used in Masresha Fetene (1985) and Yonas Feleke (1999) was used to calculate the total leaf area. Thus, the ratio of the sample leaf area (A) to the dry weight of the sample leaf (B) was used to obtain the total leaf area of the individual plant.

Total leaf area = (A/B)* total leaf dry weight

3.4.4. Biomass, biomass partitioning and root/shoot ratio

Plants were sampled during the experiment to determine biomass-partitioning responses to the different plant organs. There were two harvesting periods (first and second). The first and second harvests were made from three randomly selected plants per treatment on 42 and 56 DAP, respectively. The leaf and stem were collected before uprooting the plant so as to avoid loss of dried leaflets and other parts that would detach and fall down due to movement of the plant. The roots were collected, washed with tap water, made free of soil and passed through different diameter sieve size. Then the sampled plant organs were oven-dried at 80^0C for 24 hours to constant weight. Since biomass partitioning refers to the distribution of biomass to the different organs of the plant, the biomass of each organ is expressed as a percentage of biomass of the whole plant. Root/shoot ratio was also calculated.

3.4.5. Fine root biomass

Fine root (0.5 mm-2 mm) biomass was determined from three randomly selected plants per treatment. The growing soil in the pots was washed and allowed to pass through a 2 mm, 1 mm, 0.710 mm and 0.5 mm sieve after putting them one over the other, the largest diameter sieve being on the top. The fine roots were collected from each sieve and separated into necromass and live biomass. The sampled fine roots (necromass and live) were then oven-dried at 80 ^{0}C for 24 hours to constant weight and the dry weight was recorded.

3.4.6. Yield and yield components

At maturity (100 DAP), pod number/plant was recorded and pods from each plant in each treatment were collected. These pods were then dried in an oven at 80 ^{0}C to constant weight. Pod and seed weight per plant were recorded after threshing the pods.

3.4.7. Relative growth rate

The mean relative growth rate (RGR) was estimated following Radford (1967) as:

$$\mathbf{LnW2 - lnW_1 / t_2 - t_1}$$

Where, W_1 and W_2 are estimated organ dry weights at the first (t_1) and second (t_2) measurements of the time interval t_1 to t_2.

3.4.8. Relative water content

Leaflets from three randomly selected plants per treatment were excised and used for the estimation of relative water content (RWC). It was estimated as:

$$\mathbf{RWC = (FW\text{-}DW) / (TW\text{-}DW) * 100}$$

Where, FW is the fresh weight of the leaflets, TW is the turgid weight of the leaflets floated on distilled water in petridish for 24 hours and DW is the dry weight of the leaflets oven dried at 80 ^{0}C to constant weight.

3.4.9. Chlorophyll a fluorescence

Chlorophyll fluorescence measurements were made on attached 3rd and 4th upper most fully expanded leaf using portable fluorometer (plant efficiency analyzer (PEA), Hansatech Instruments Ltd, Kings Lynn, Norfolk, England). Prior to each measurement, leaf samples were dark adapted for 30 minutes with a small, lightweight leaf clips. The leaf clips are constructed from white plastic to minimize the effects of heat build up on the leaf during the period the leaf clip is in place. Illumination was provided by six high intensity light emitting diodes (LEDs) which are focused onto the leaf surface to provide even illumination over the exposed area of the leaf. LEDs provide red light of a peak wavelength of 650 nm, which is readily absorbed by the chloroplasts of the leaf. The sensor unit’s central photodiode absorbs the fluorescence and automatically calculates the fluorescence indices Fo, Fm, Fv and Fv/Fm, where Fo and Fm are minimum and maximum fluorescences of dark-adapted leaf, respectively and Fv/Fm is the maximum quantum yield of PS II which is a measure of efficiency of open PS II (Schreiber et al., 1994).

Light adapted chlorophyll fluorescence measurements were made at the natural leaf angle using a pulse amplitude modulated fluorometer (MINI-PAM, Walz, Effltrich, Germany). The fluorometer fiberoptic was placed at a 60^0 angle to the leaf blade attached with leaf clip holder

(2030-B, Henz, Walz). The leaf clip is equipped with sensors for simultaneous recording of photosynthetically active radiation (PAR) and thermocouple monitoring leaf temperature (NiCr-Ni). The effective quantum yield of PS II, which is a measure of the efficiency of closed PS II units was estimated as $\Phi PS\ II = (\Delta F)/Fm'$ (Schreiber et al., 1994) where F is the minimum fluorescence yield measured before a short pulse of saturating light and Fm' is the maximum fluorescence yield measured during a short pulse of saturating light. Electron transport rate (ETR) was calculated as $\Phi PS\ II*PAR*0.5*0.84$ (Schreiber et al., 1994) where 0.5 is assumed as fraction of the excitation energy absorbed by PS II and 0.84 is as the fractional light absorption of the leaf.

3.4.10. Statistical analysis

All the data collected were subjected to analysis of variance (ANOVA) test (SPSS/Pc_{+}, statistical package, and version 10). Multiple comparisons of means were carried out using Tukey's Honestly Significant Difference (HSD) at $p < 0.05$.

4. RESULTS

4.1. Vegetative growth

The interactive effects of water deficit and phosphorus deficiency on leaf number, plant height, total leaf area, relative growth rate (RGR) and biomass accumulation of three chickpea accessions (Yaya Gulele, Legambo and Moretena Jiru) were investigated. The effect of these stress factors on leaf number is shown in Table 2. In chickpea plants of accession Moretena Jiru, leaf number was significantly higher in normal phosphorus-low water stressed (NP-LWS) than normal phosphorus-moderate water stressed (NP-MWS) and normal phosphorus-severe water stressed (NP-SWS) chickpea plants. Plants of accession Moretena Jiru had also significantly greater number of leaves under NP-LWS than low phosphorus-severe water stress (LP-SWS) chickpeas. Fifty-six days after planting, leaf number was significantly lower in NP-MWS, NP-SWS and LP-SWS treated plants by 17, 34, and 34%, respectively. In the other two accessions, the differences in leaf number among treatments were not significant.

As shown in Table 2, different levels of water and phosphorus in the various chickpea accessions affected plant height. Accession Yaya Gulele chickpea plants under NP-LWS had the longest plant height while plants of accession Legambo under NP-SWS and LP-SWS treatments achieved the shortest. Visible differences in plant height were observed between normal phosphorus and low phosphorus treatments under the different water stress levels at the last sampling day (56 DAP). However, none of these differences were found to be significant ($p<0.05$). The differences in plant height and leaf number between treatments in all accessions were small at 42 DAP (14 days after the induction of water stress). However, differences became greater as the duration of the stress was prolonged and continued to act upon chickpea plants (56 DAP).

On the other hand, total leaf area under LP-LWS, LP-MWS and LP-SWS treated plants was lower than the corresponding NP-LWS, NP-MWS and NP-SWS treatments (Fig. 1). It was lower by 39, 22 and 8% in plants of accession Yaya Gulele and by 27, 9 and 16% in plants of accession Legambo. Total leaf area was also lower by 21, 12 and 13% in plants of accession Moretena Jiru under LP-LWS, LP-MWS and LP-SWS treatments, respectively. Comparatively, accessions Yaya Gulele and Moretena Jiru had the highest and lowest total leaf area, respectively, under all treatments, 56 DAP. Nevertheless, the observed differences among accessions and treatments were not significant ($p<0.05$).

Table: 2. Leaf number and plant height of three chickpea accessions subjected to different water and phosphorus levels at the vegetative stage. (n = 4)

Treatments	**Leaf number**			**Plant height (cm)**		
	Yaya Gulele	Legambo	Moretena Jiru	Yaya Gulele	Legambo	Moretena Jiru
NP-LWS	25_a	22.7_a	27.7_a	34.3_a	33_a	32.7_a
NP-MWS	20_a	17_a	23_b	32_a	26_a	30_a
NP-SWS	19_a	18.3_a	18.3_b	27.2_a	19.7_a	28.8_a
LP-LWS	19_a	21.7_a	22.3_a	32.7_a	33.3_a	31.3_a
LP-MWS	20_a	22_a	22.3_a	32_a	27_a	28_a
LP-SWS	19.7_a	16.7_a	18.3_b	28.3_a	20.7_a	28_a

* Means within the same column followed by different letters are significantly different at $p< 0.05$ determined by Tukey’s Honestly Significant Difference.

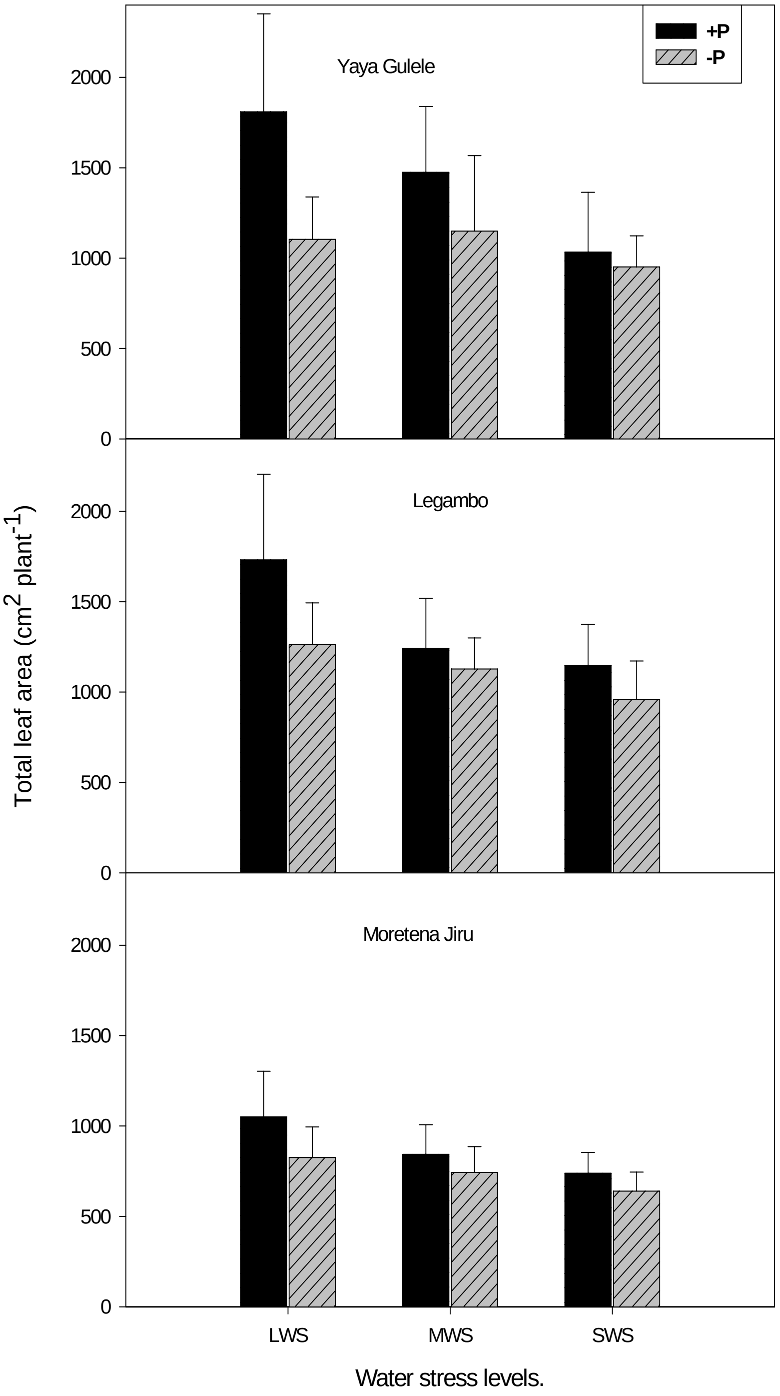

Fig. 1. Total leaf area of three chickpea accessions subjected to three water regimes and two levels of phosphorus at the vegetative stage (28 DAP). Bars indicate S. E. of the means. (n = 8).

Relative growth rates of chickpea accessions were positive in almost all plant organs under all treatments as shown in Table 3 and Table 4. However, stem in accession Legambo under LP-LWS, root in accession Moretena Jiru under NP-SWS, LP-LWS, LP-MWS and LP-SWS showed negative relative growth rates. Fine roots in plants of accession Legambo under NP-LWS, NP-MWS and LP-MWS and in accession Yaya Gulele under LP-SWS showed negative relative growth rates. The differences in RGR among accessions and treatments were not significant.

Biomass partitioned to the different plant parts (leaf, stem and root) of chickpea plants in the three accessions and under different treatment groups on 56th DAP is presented in Fig. 2. Leaf biomass decreased by 4.2 and 8.4% under LP-MWS and LP-SWS treatments in accession Yaya Gulele, respectively as compared to normal phosphorus and the corresponding water stress levels (Fig. 2a). It was also lower by 22.2 and 4% under LP-LWS and LP-MWS in accession Legambo and 7.7, 4.2 and 8.7% under LP-LWS, LP-MWS and LP-SWS conditions in plants of accession Moretena Jiru, respectively as compared to normal phosphorus and the corresponding water stress levels (Fig. 2b, c). In the same way, stem biomass decreased by 5.6% in accession Yaya Gulele under LP-SWS; 9.5, 14.3 and 18.1% in accession Legambo under LP-LWS, LP-MWS and LP-SWS and 12.5% in accession Moretena Jiru under LP-LWS treatments, respectively (Fig. 2d, e, f). However, root biomass showed a reverse pattern except for chickpea plants of accession Moretena Jiru. Root biomass increased by 10, 26 and 5% in plants of accession Yaya Gulele and 6.7, 6.3 and 5.9% in plants of accession Legambo under LP-LWS, LP-MWS and LP-SWS treatments, respectively when compared with NP-LWS, NP-MWS and NP-SWS (Fig. 2g, h). In accession Moretena Jiru, root dry weight diminished by 20,15 and 7.7% under LP-LWS, LP-MWS and LP-SWS, respectively (Fig. 2i). In general, chickpea accessions grown under normal phosphorus conditions accumulated most of their dry weight to the leaf followed by stem, while those grown under low phosphorus treatments accumulated a larger proportion of their dry weight to the root part (Fig. 2). The differences in dry weight of plant organs were not significant ($p<0.05$) among accessions and treatments. However, root dry weight in plants of accession Moretena Jiru was statistically significant ($p<0.05$) between NP-MWS and other low phosphorus treatments (LP-LWS, LP-MWS and LP-SWS). In addition, an increased fine root biomass was observed under low phosphorus treatments, although not significant (Fig. 2j, k, l).

Root/shoot biomass ratio responses of chickpea accessions under the different treatments are shown in Fig. 3. A higher root/shoot biomass ratio was observed under water stressed and phosphorus deficient chickpea plants of accessions Yaya Gulele and Legambo. The reverse was true for chickpea plants of accession Moretena Jiru. Chickpea plants of accession Yaya Gulele had the highest root/shoot biomass ratio followed by plants of accession Legambo under LP-LWS and LP-SWS conditions (Fig. 3), whereas the lowest root/shoot biomass ratio was recorded in chickpea plants of accession Moretena Jiru under LP-MWS (Fig. 3).

Water deficit stress and phosphorus deficiency had no significant difference on percentage biomass partitioning to the leaf, stem and root among accessions and between treatments as shown in Fig. 4. About 34-37, 33-39 and 34-43% of the total plant biomass was partitioned to the leaf in chickpea plants of accessions Yaya Gulele, Legambo and Moretena Jiru, respectively (Fig. 4a, b, c) at 56 DAP. The stem contributed 28-36, 27-35 and 30-34% of the total plant biomass in chickpea plants of accessions Yaya Gulele, Legambo and Moretena Jiru, respectively (Fig. 4d, e, f). Similarly, 28-37, 30-36 and 23-36% of the total plant biomass was partitioned to the root in the order of accessions mentioned above (Fig. 4g, h, i).

Table: 3. Relative growth rate of leaf and stem of three chickpea accessions subjected to three levels of water and two levels of phosphorus at vegetative stage; Samples were taken 42 and 56 DAP. (n = 3-4).

	Leaf (g day^{-1})			**Stem (g day^{-1})**		
Treatments	Yaya Gulele	Legambo	Moretena Jiru	Yaya Gulele	Legambo	Moretena Jiru
NP-LWS	0.004±0.004	0.006±0.002	0.006±0.003	0.002±0.005	0.003±0.005	0.007±0.005
NP-MWS	0.005±0.003	0.005±0.001	0.004±0.002	0.011±0.003	0.005±0.004	0.005±0.001
NP-SWS	0.002±0.002	0.004±0.002	0.003±0.001	0.005±0.005	0.006±0.001	0.001±0.002
LP-LWS	0.004±0.004	0.005±0.002	0.004±0.002	0.006±0.003	-.0001±.002	0.005±0.002
LP-MWS	0.001±0.001	0.004±0.002	0.004±0.005	0.012±0.001	0.006±0.005	0.004±0.003
LP-SWS	0.001±0.004	0.003±0.003	0.003±0.001	0.004±0.003	0.003 ± 0	0.002 ± 0.0

* Means within the same column are not significantly different at $p<0.05$ as determined by Tukey's HSD method.

Table: 4. Relative growth rate of root (coarse and fine roots) and fine roots of three chickpea accessions subjected to three levels of water and two levels of phosphorus at vegetative stage; Samples were taken 42 and 56 DAP. (n = 3-4).

	Root (g day^{-1})			**Fine roots (g day^{-1})**		
Treatments	Yaya Gulele	Legambo	Moretena Jiru	Yaya Gulele	Legambo	Moretena Jiru
NP-LWS	0.003±0.002	0.001±0.002	0.001±0.001	0.005±0.002	0.001±.004	0.003 ± 0.0
NP-MWS	0.002±0.001	0.001±0.001	0.006±0.004	0.005±0.003	-0.001±.002	0.00 ± 0.002
NP-SWS	0.005±0.004	0.006±0.002	-0.001±.006	0.006±0.002	0.00 ± 0.003	0.00 ± 0.002
LP-LWS	0.008±0.001	0.005±0.003	-0.004±.006	0.005±0.003	0.001±0.003	0.002±0.007
LP-MWS	0.008±0.004	0.004±0.003	-0.001±.002	0.001±0.004	-0.001±.001	0.001±0.001
LP-SWS	0.001±0.001	0.004±0.001	-0.005±.005	-0.002±.002	0.00 ± 0.001	0.001±0.001

* Means within the same column are not significantly different at $p<0.05$ as determined by Tukey's HSD method.

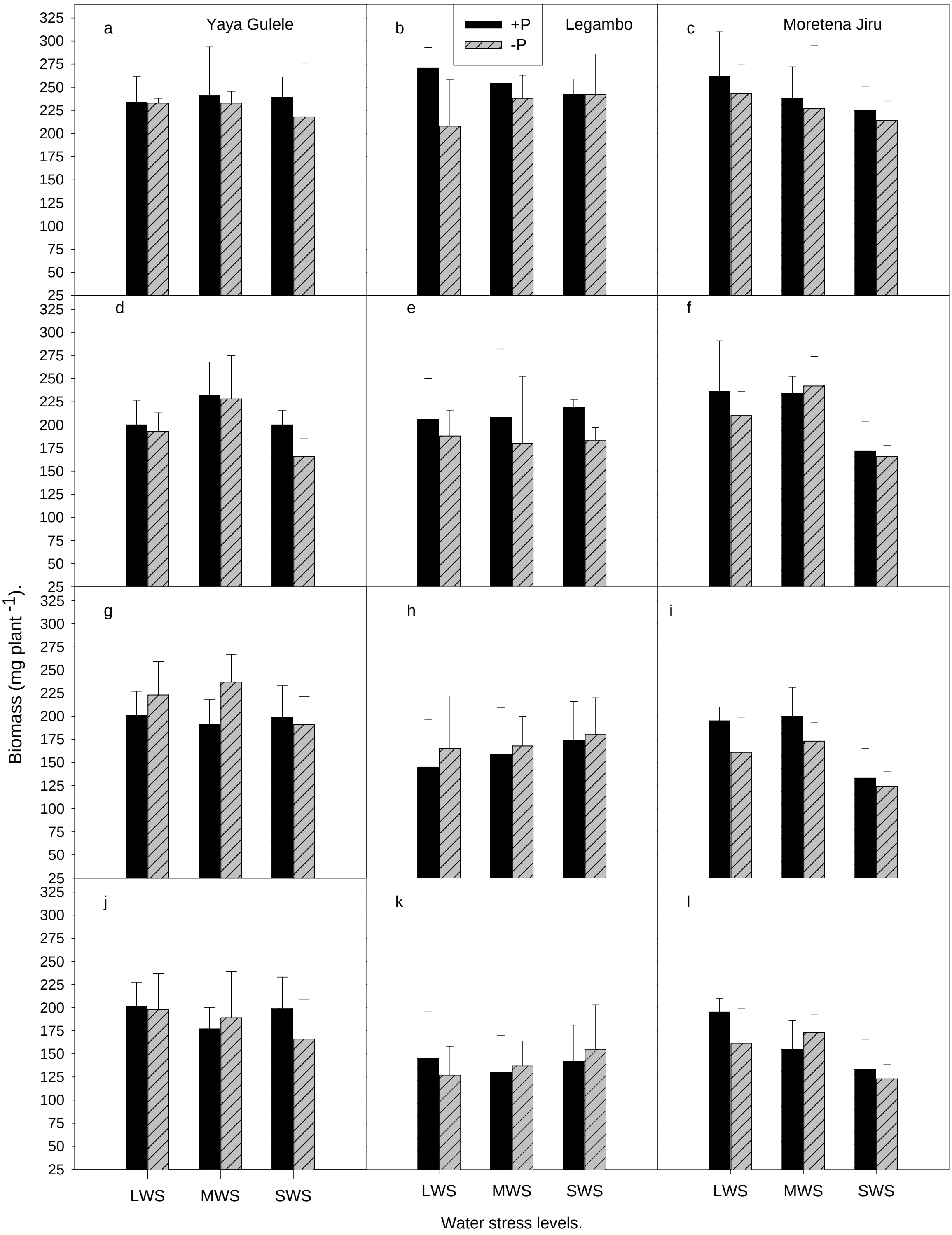

Fig. 2. Biomass of the leaf (a, b and c), stem (d, e and f), root (coarse and fine roots) (g, h and i) and fine root (j, k and l) of three chickpea accessions under three water regimes and two phosphorus levels induced at vegetative stage. (56 DAP). Bars indicate S. E of the means. (n = 3-4).

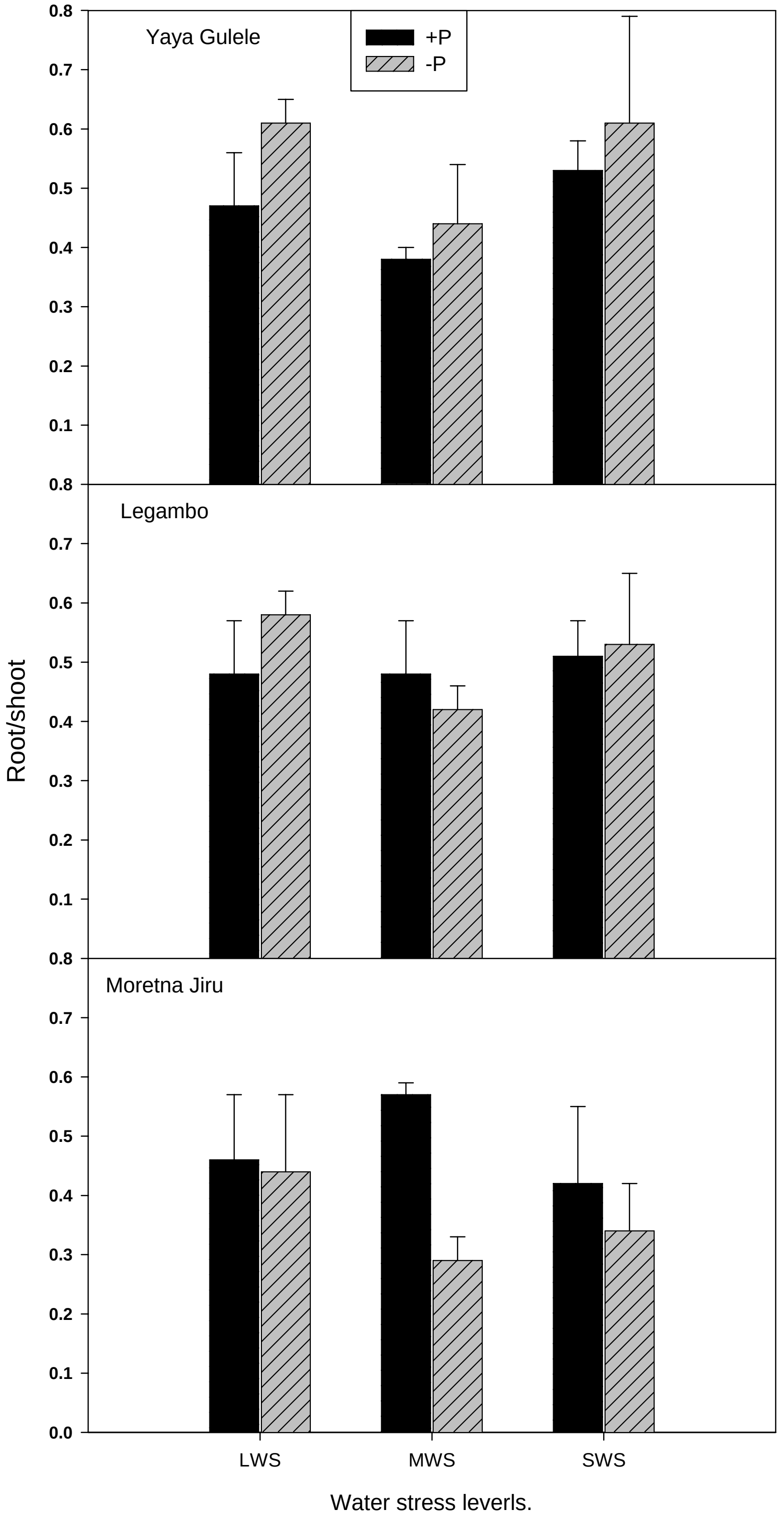

Fig. 3. Root/shoot biomass ratio of three chickpea accessions subjected to three water regimes and two levels of phosphorus at the vegetative stage.Bars indicate S. E of the means. (n = 3).

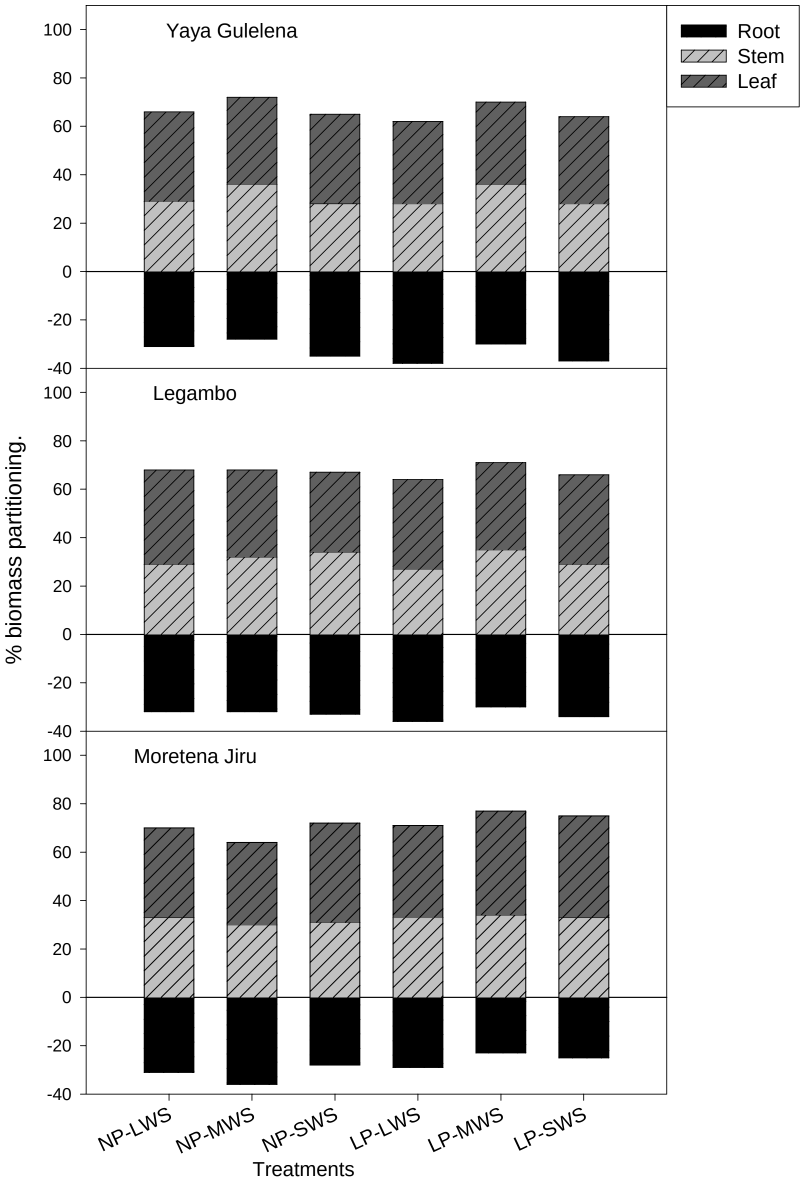

Fig. 4. Percent biomass partitioned to the leaf, stem and root parts of three accessions of chickpea plants subjected to moisture stress at two phosphorus levels at vegetative stage. Bars indicate S. E of the means (n = 3).

4.2. Water relations

Leaf relative water content (RWC) was relatively lower in chickpea plants for moisture stress induced at the flowering stage than those at the vegetative stage (Fig. 5 and 6). For drought induced at vegetative stage, chickpea plants of accession Legambo were exceptional in that they showed a significant difference in RWC at midday (leaf samples taken at 12:00 h) between NP-LWS and LP-SWS, NP-SWS and LP-MWS, NP-SWS and LP-SWS (Fig. 6a). Moreover, midday RWC in chickpea plants of accession Moretena Jiru was significantly higher than chickpea plants of accession Legambo under LP-MWS conditions. For drought induced at flowering stage, there were no statistically significant RWC differences between treatments. However, chickpea plants of accession Yaya Gulele had a higher predawn (leaf samples taken before sun rise) RWC than plants of accession Moretena Jiru under LP-MWS (Fig. 5b). In all cases, normal phosphorus treatments had an improved RWC than low phosphorus treatments. In addition, predawn RWC (Fig. 5) was higher than midday RWC (Fig. 6) under most treatments.

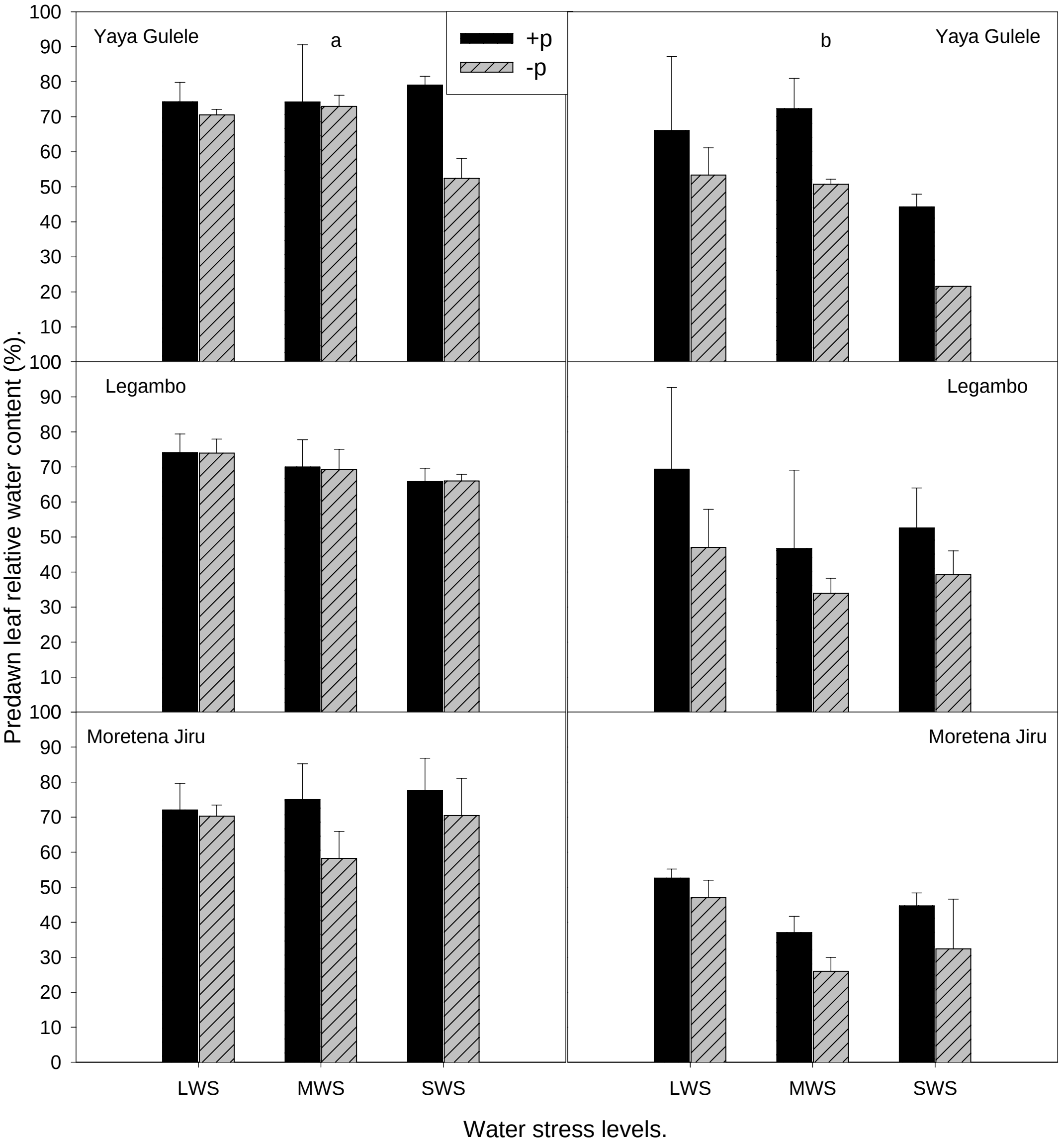

Fig. 5. Leaf relative water content (RWC) at predawn in chickpea plants of three accessions subjected to different levels of moisture stress and phosphorus levels during vegetative (a) and flowering (b) stages.
Bars indicate S. E of the means. (n = 3-5).

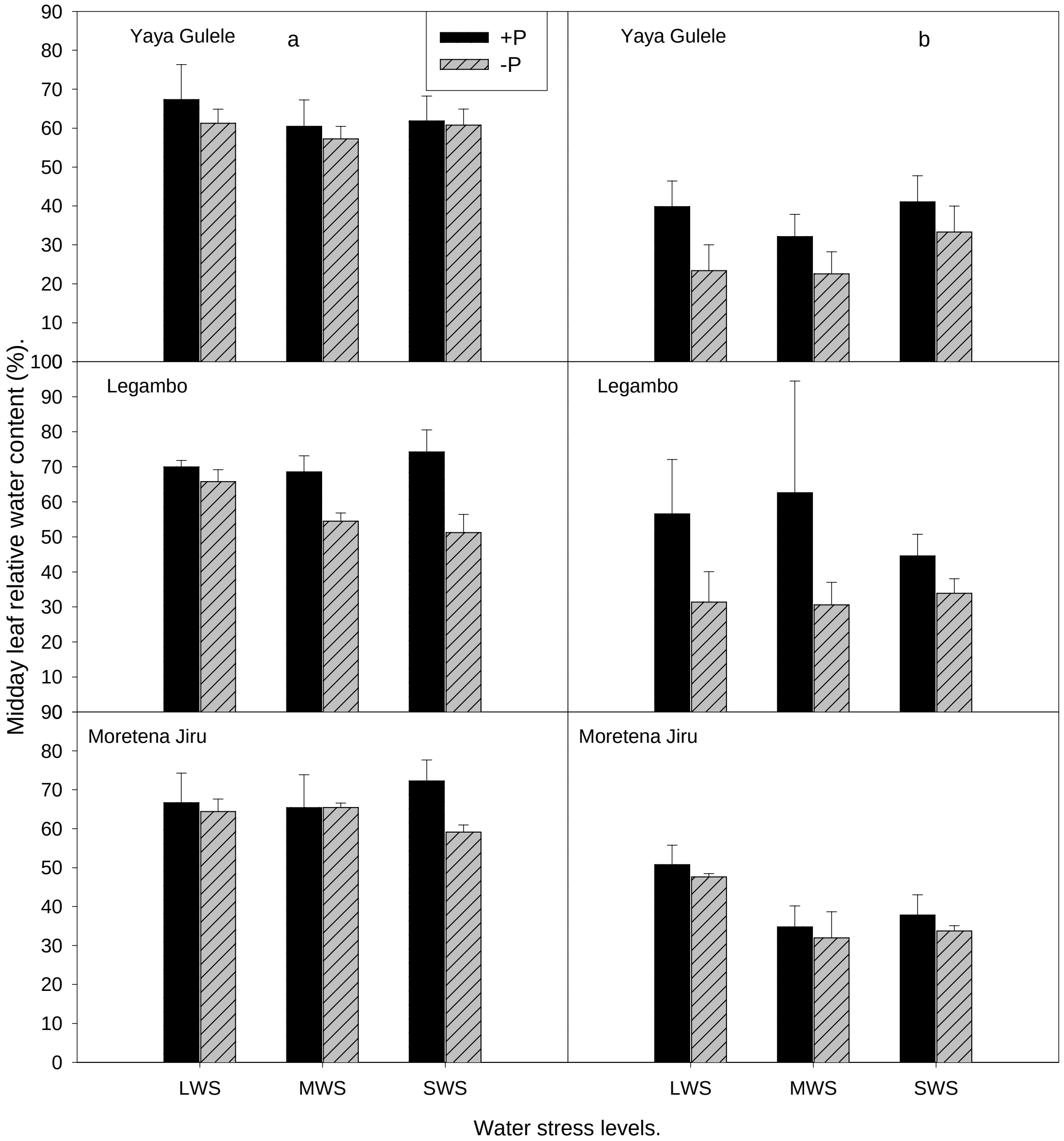

Fig. 6. Leaf relative water content (RWC) at midday in chickpea plants of three accessions subjected to differing levels of moisture stress and phosphorus levels during vegetative (a) and flowering stages. Bars indicate S. E.(n = 3-5).

4.3. Chlorophyll a fluorescence

Fluorescence measurements were made to find out the diurnal variation in fluorescence responses at vegetative stage of different accessions under different treatments. Although significant differences were not observed across all treatments in all accessions, fluorescence responses of plants from accessions Yaya Gulele and Legambo that received NP-SWS treatment showed significant differences at 10:00 and 12:00 h. (Fig. 8a). In the flowering stage, significant differences in Fv/Fm ratio were observed only among treatments in plants of accession Moretena Jiru at 10:00 and 18:00 h. On the other hand, significant differences in Fv/Fm ratio were observed for responses at 10:00 h between accession Yaya Gulele and Legambo, Yaya Gulele and Moretena Jiru under NP-SWS treatment (Fig. 8b). In addition, when comparing 14:00 h maximal quantum yield of PS II among accessions and treatments (Fig. 7), a higher Fv/Fm ratio was observed under NP-LWS as compared to all other treatments and a lower value was recorded for NP-MWS treatments of accession Yaya Gulele (Fig. 7a). During the day, a general reduction in the maximal quantum yield of PS II was seen between 12:00-14:00 h in all accessions under all treatments (Fig. 8). However, a recovery from this decline was observed after 16:00 h, which revealed that plants were not irreversibly photoinhibited.

The effective quantum yield of PS II given by ΔF/Fm’ of light adapted leaf samples provides an estimation of the proportion of light absorbed by chlorophyll used in PS II photochemistry. This parameter exhibited a higher value in plants that received normal phosphorus treatments than their low phosphorus counterparts. For plants in the vegetative stage, significant differences in ΔF/Fm’ were observed among accessions. Effective quantum yield at 18:00 h was significantly higher in accession Moretena Jiru under LP-SWS treatments than the other accessions. Similarly, accession Yaya Gulele had greater ΔF/Fm’ ratio at 18:00 h than accession Legambo under LP-LWS treatments. In addition, plants that received NP-LWS and NP-MWS treatments respond differently from all other treatments (NP-SWS, LP-LWS, LP-MWS and LP-SWS) at 14:00 h (Fig. 10a) and these differences were significant ($p<0.05$). At the flowering stage, ΔF/Fm' measurements of 10:00 h were significantly higher in plants that received NP-SWS treatment as compared to those treated with LP-SWS plants of accession Yaya Gulele. This parameter measured at 8:00 h was also significantly higher for plants under NP-LWS treatment as opposed to those that received NP-SWS and LP-SWS treatments of accession Legambo (Fig. 10b). The effective quantum yield performance at 14:00 h of chickpea accessions under the various treatments is presented in Fig. 9 and the diurnal change is shown in Fig. 10.

Generally, differences in electron transport rate (ETR) among accessions and treatments were significant. In the vegetative stage, chickpea plants of accession Yaya Gulele that received normal phosphorus treatments (NP-LWS, NP-MWS and NP-SWS) generally had higher ETR than those treated with low phosphorus (LP-LWS, LP-MWS and LP-SWS). Moreover, the performance at 10:00 h of plants of this accession under LP-LWS and LP-MWS treatments was significantly different from those treated with LP-SWS plants. On the other hand, under NP-SWS condition, plants of accession Moretena Jiru had a lower ETR than plants of the other two accessions. Under LP-SWS, plants of accession Moretena Jiru had significantly greater ETR than plants of accession Yaya Gulele at 8:00 and 16:00 h. In the flowering stage, chickpea plants of accession Yaya Gulele treated with NP-SWS and LP-MWS were significantly greater from those under LP-SWS and LP-SWS treatments, respectively at 8:00 h of the day, but those treated with NP-MWS were significantly lower than those treated with LP-MWS. In addition, ETR of plants of accession Moretena Jiru, which were treated with NP-MWS were significantly lower from those under LP-MWS at 10:00 h due to phosphorus deficiency. At 10:00 h of the day, plants of accession Moretena Jiru had a higher ETR than plants of accession Yaya Gulele under NP-LWS.

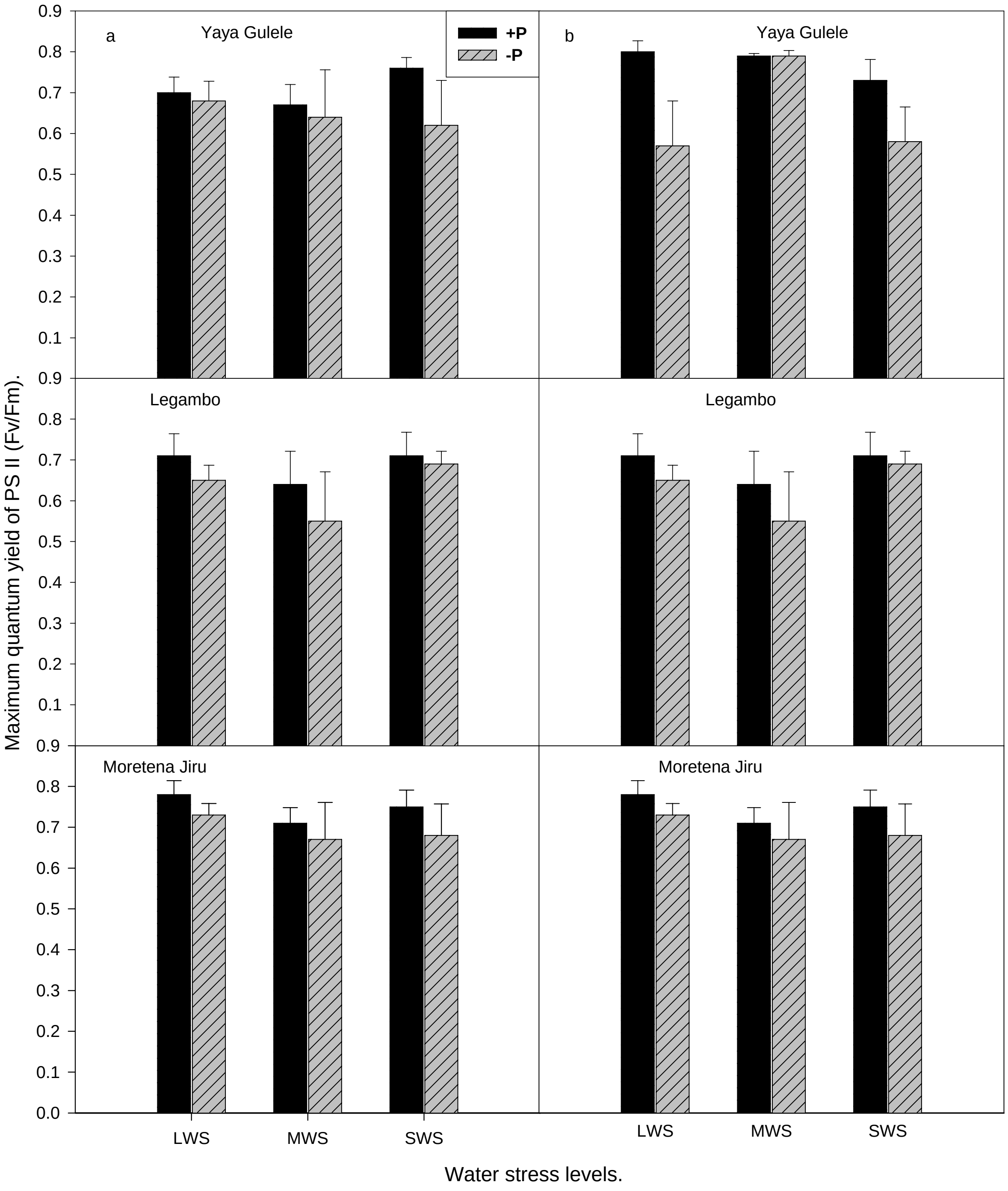

Fig. 7. Maximal quantum yield of PS II (Fv/Fm) of three chickpea accesssions subjected to three levels of moisture stress and two levels of phosphorus during the vegetative (a) and flowering (b) stages. Bars indicate S. E. of the means. (n = 2-4).

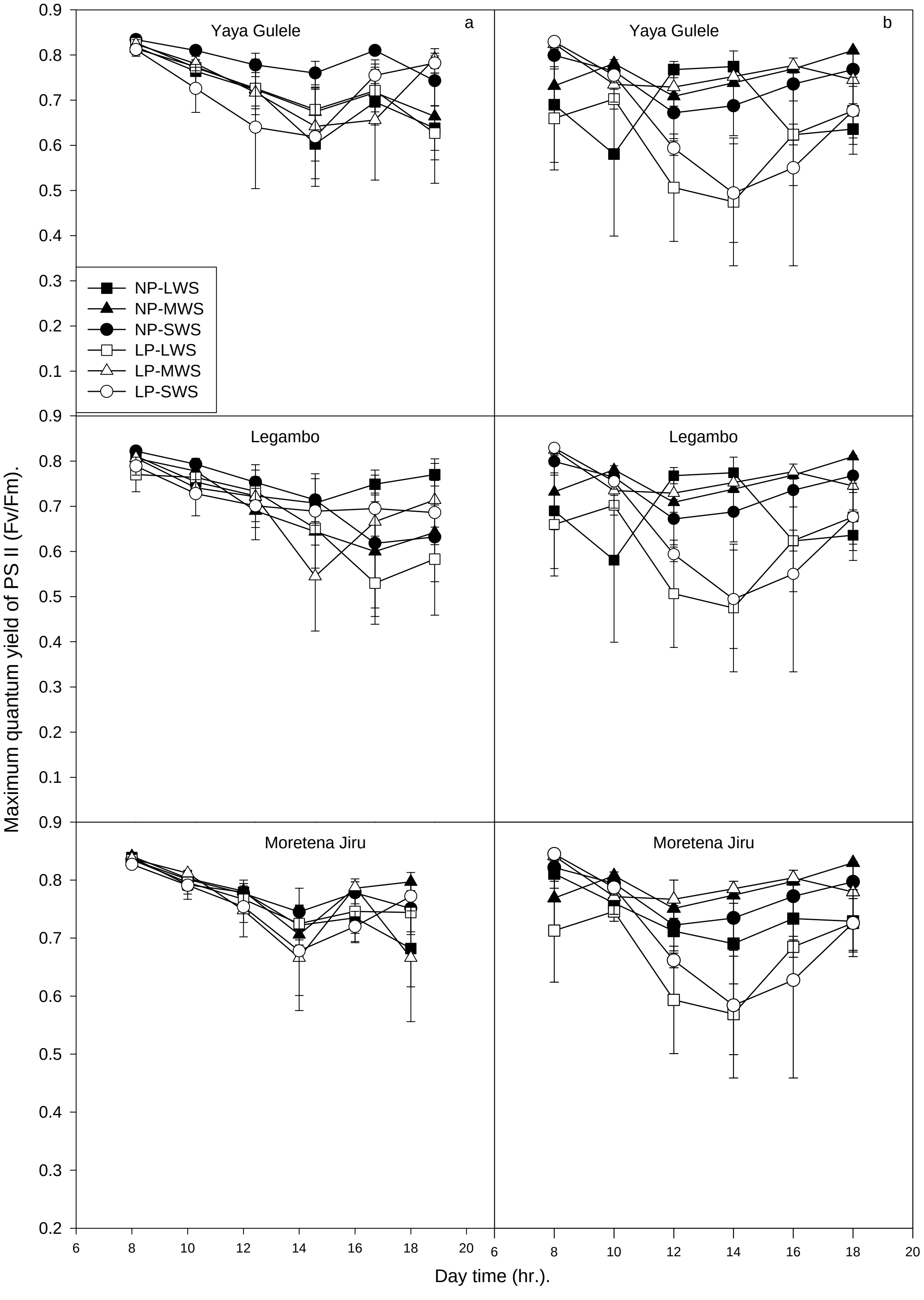

Fig. 8. Diurnal change in maximal quantum yield (Fv/Fm) of three chickpea accessions under different water and phosphorus levels induced at vegetative (a) and flowering (b) stages. Bars indicate S. E. of the means. (n = 2- 4).

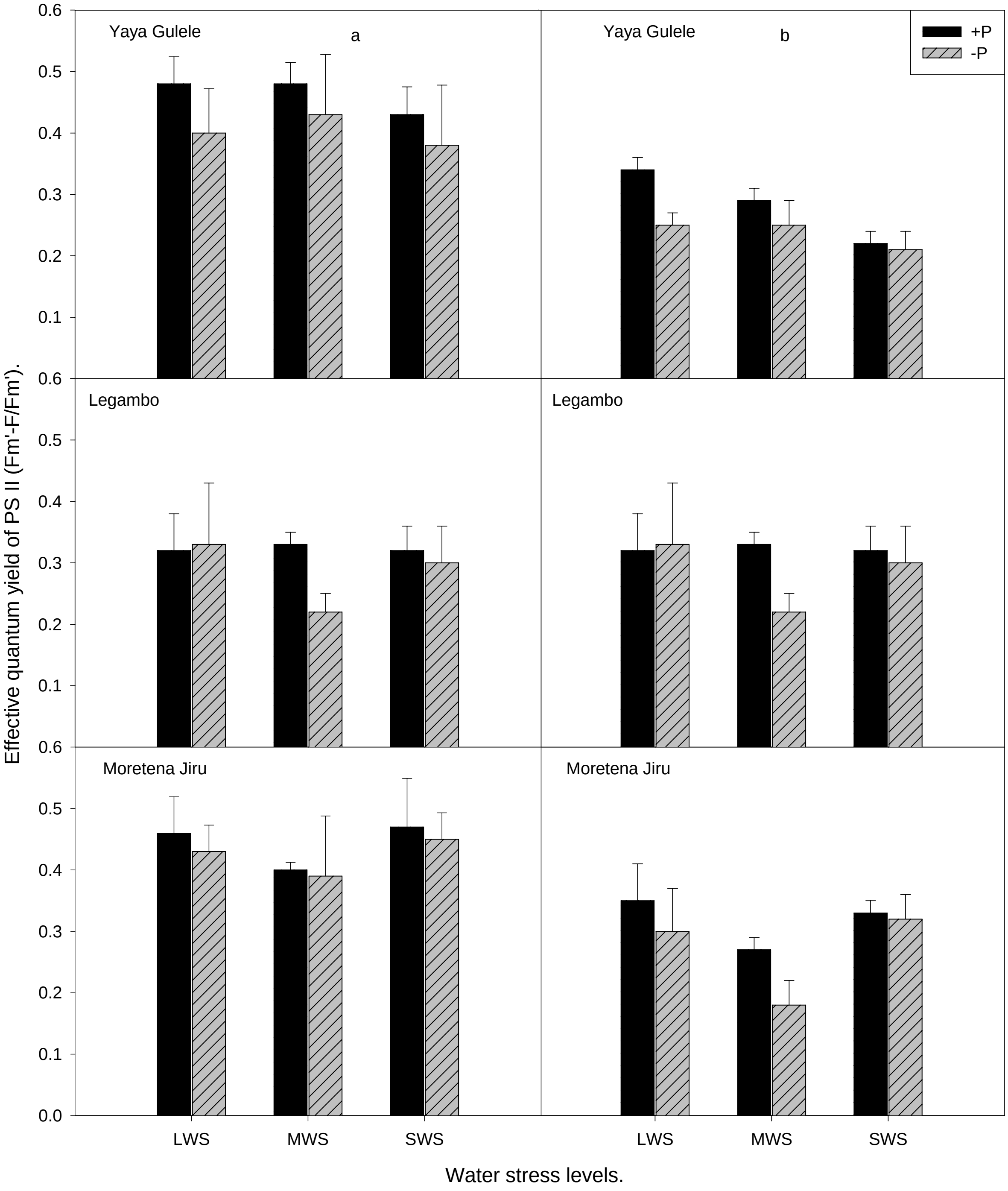

Fig. 9. Effective quantum yield of PS II (Fm'-F/Fm') of three chickpea accessions subjected to three water and two phosphorus levels at vegetative (a) and flowering (b) stages. Bars indicate S. E. of the means. (n = 2-4).

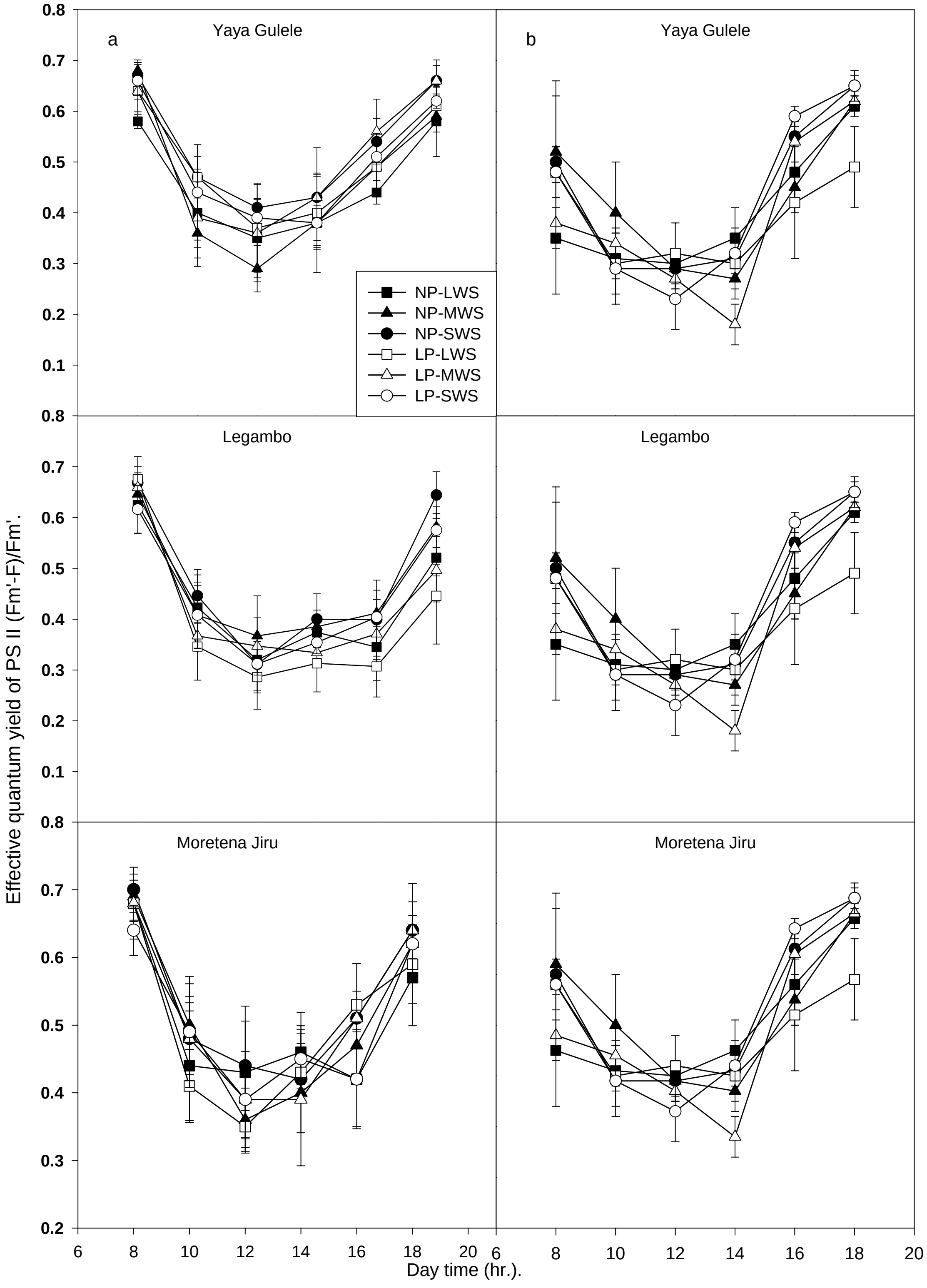

Fig. 10. Diurnal change in effective quantum yield of PS II (ΔF/Fm') of three chickpea accessions subjected to three water and two phosphorus levels at vegetative (a) and flowering (b) stages. Bars indicate S. E. of the means. (n = 2-4).

4.4. Yield and yield components

Yield and yield component responses of the three chickpea accessions are shown in Fig. 11, 12 and 13. In the present study, accession Legambo was the first to flower, 7 days after the induction of water stress. Visible differences in yield and yield components were observed among treatments and accessions. However, for drought imposed at vegetative stage, significantly higher numbers of pods were produced by plants of accession Legambo treated with NP-LWS than those treated with NP-SWS, LP-MWS and LP-SWS. Similarly, plants of accession Moretena Jiru produced significantly higher number of pods when treated with NP-LWS than those treated with NP-SWS and LP-SWS (Fig. 11a). For drought imposed at flowering stage, pod number was the only yield component that showed significant differences among treatments in all accessions (Fig. 11b). Chickpea plants of accession Yaya Gulele treated with NP-LWS had significantly higher number of pods than those treated with LP-SWS. Statistically significant ($p<0.05$) differences were also observed for plants in accession Legambo among all treatments. Similar results were observed between accessions under the different treatments. Accordingly, accession Legambo had significantly greater number of pods than accession Yaya Gulele under LP-LWS and accession Moretena Jiru under NP-LWS, NP-MWS and LP-LWS treatments (Table. 5). In addition, pod weight was significantly higher in accession Yaya Gulele under NP-LWS and LP-LWS and lower under LP-SWS than the other accessions (Fig. 12b). Moreover, seed weight was significantly higher in accession Yaya Gulele under NP-LWS and LP-LWS conditions than accession Legambo and Moretena Jiru (Fig. 13b).

Table: 5. Yield and yield components of three chickpea accessions subjected to three moisture stress and two phosphorus levels at the flowering stage.

Treatments	**Pod number**			**Pod weight (g/plant)**			**Seed weight (g/plant)**		
	Yaya Gulele	Legambo	Moretna Jiru	Yaya Gulele	Legambo	Moretna Jiru	Yaya Gulele	Legambo	Moretna Jiru
NP-LWS	2.167	3.5_{a}	1.167_{b}	0.038_{a}	0.04_{b}	0.016	0.122_{a}	0.107_{b}	0.033
NP-MWS	1.167	2.333_{a}	0.667_{b}	0.014	0.05	0.007	0.055	0.071	0.019
NP-SWS	0.5	1.5	0.667	0.0043	0.011	0.005	0.014	0.053	0.029
LP-LWS	1.833_{a}	2.667_{b}	1_{a}	0.03_{a}	0.028_{b}	0.016_{b}	0.09_{a}	0.057_{b}	0.03_{b}
LP-MWS	1	1.167	0.33	0.0147	0.012	0.004	0.04	0.046	0.007
LP-SWS	0.167	1.5	0.5	0.002_{a}	0.018_{b}	0.014_{b}	0	0.042	0.004

* For each parameter, means within the same row followed by different letters are significantly different at $p < 0.05$ as determined by Tukey's HSD.

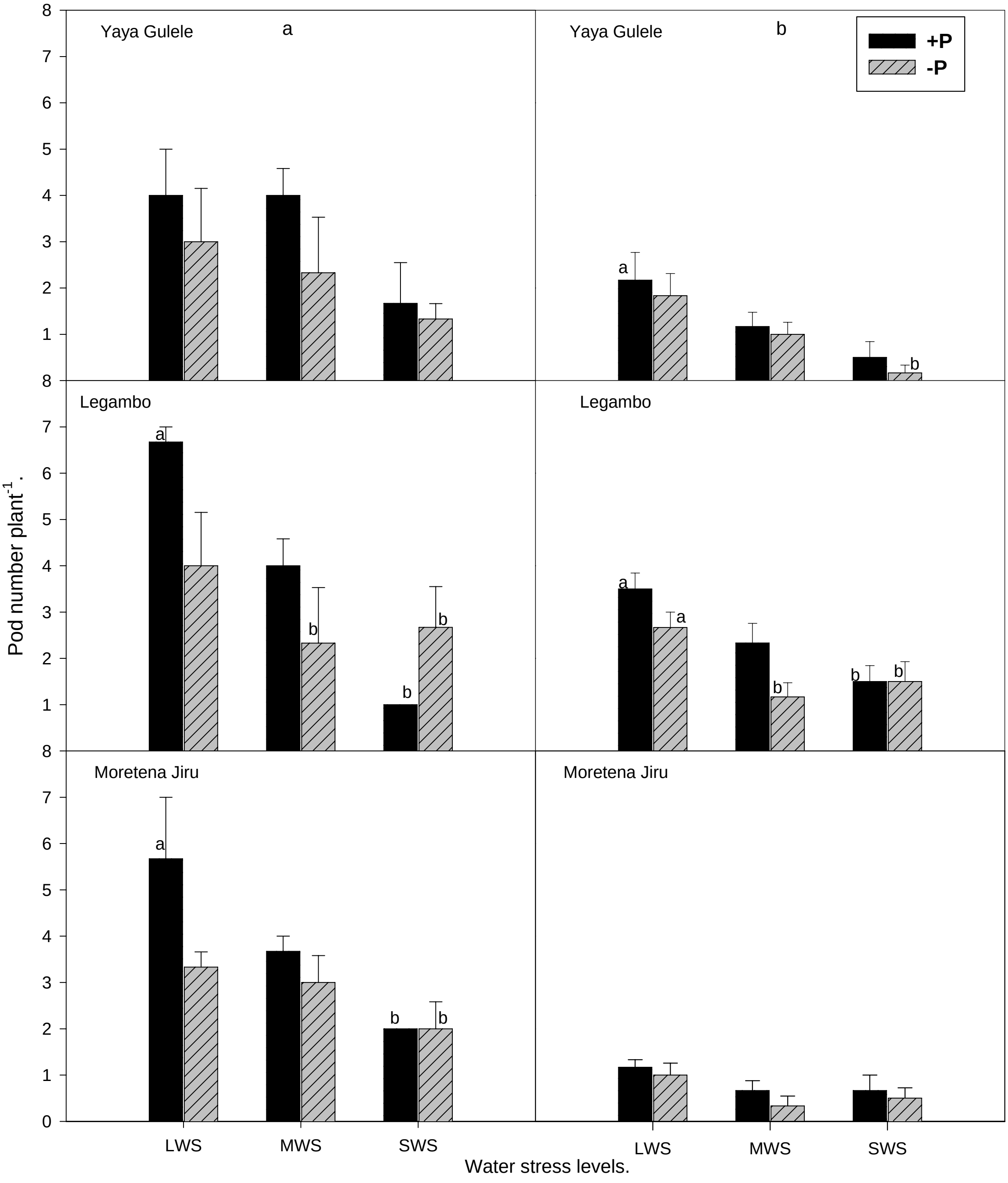

Fig. 11. Pod number in three chickpea accessions subjected to three levels of moisture stress and two levels of phosphorus at vegetative (a) and flowering (b) stages. Bars indicate S. E. of the means (n = 3 - 6).

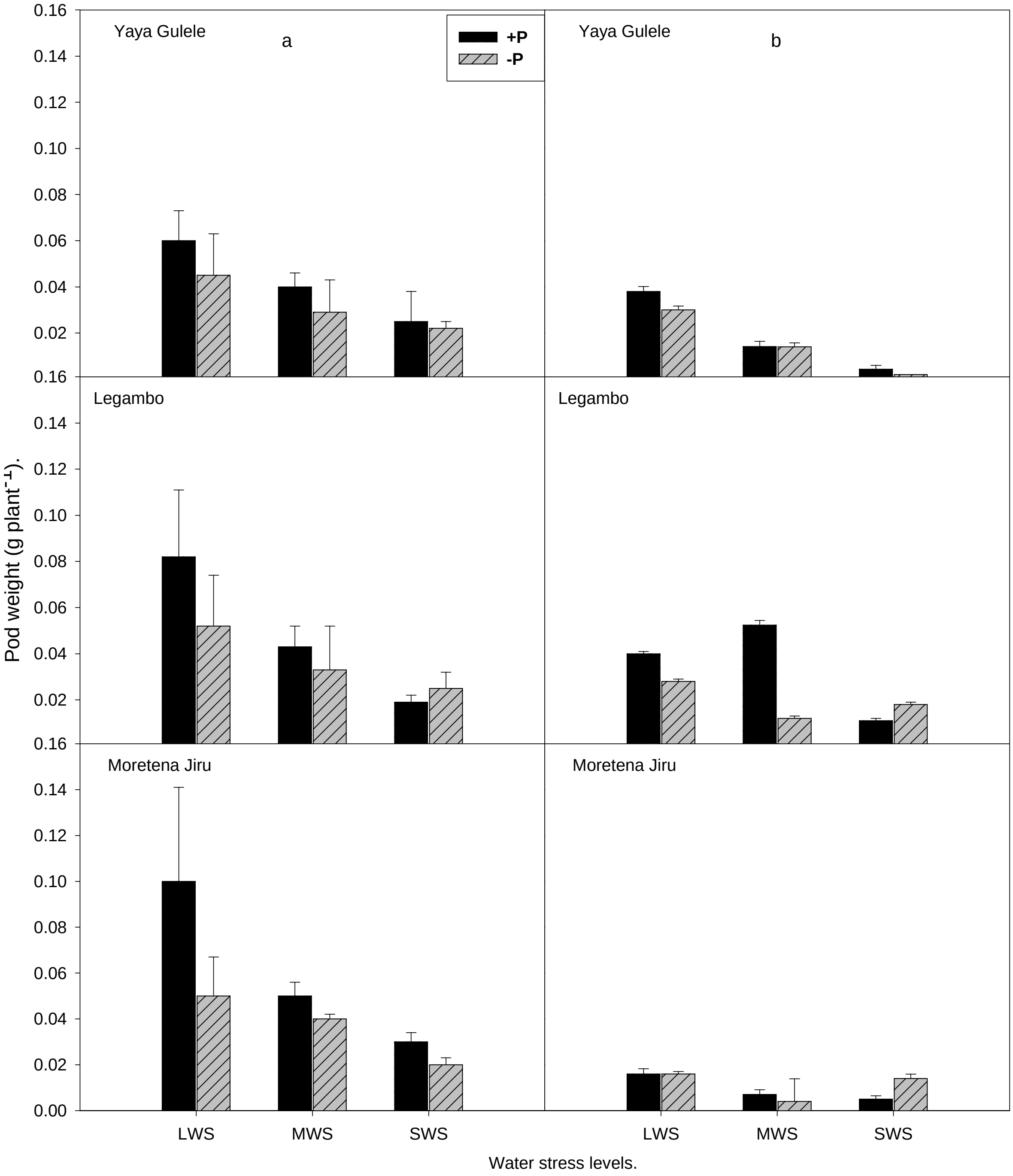

Fig. 12. Weight of pods in three chickpea accessions subjected to three levels of moisture stress and two levels of phosphorus at vegetative (a) and flowering (b) stages. Bars indicate S. E.the means (n = 3 - 6).

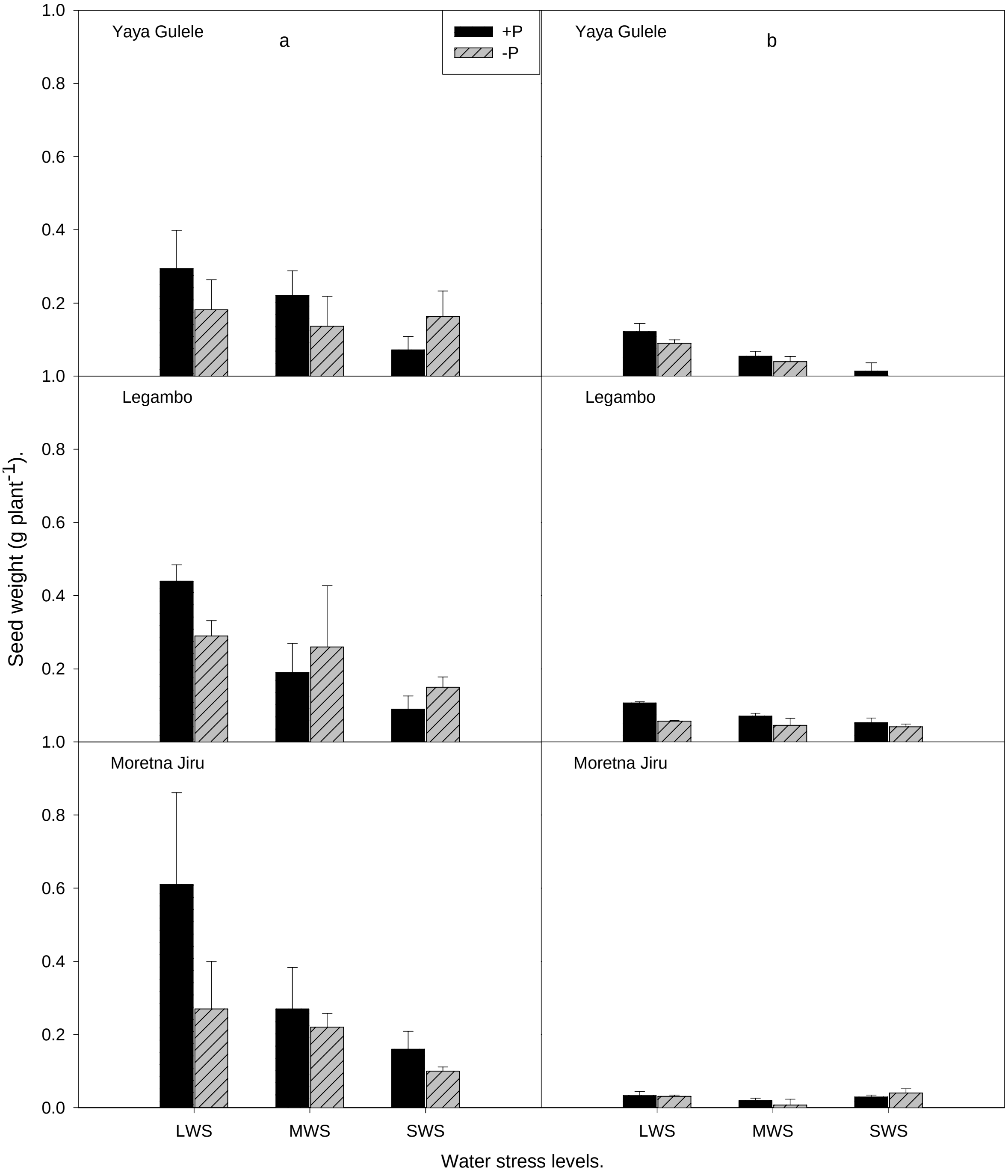

Fig. 13. Seed weight of three chickpea accessions subjected to three levels of moisture stress and two levels of phosphorus at vegetative (a) and flowering (b) stages. Bars indicate S. E. of the means (n = 3 - 6).

5. DISCUSSION

5.1. Plant growth

In the present study, a decline in vegetative growth (leaf number, plant height, total leaf area and biomass) was observed under water stressed and phosphorus deficient chickpea plants of all accessions, except that root biomass showed the reverse. There were visible differences in leaf number among treatments and accessions. However, these differences were not high enough to produce significant differences in plants of Yaya Gulele and Moretena Jiru (Table 2). Statistically significant differences were observed only in chickpea plants of accession Moretena Jiru. Plants of accession Moretena Jiru grown under NP-LWS had significantly greater number of leaves than those grown under NP-MWS, NP-SWS and LP-SWS conditions. The significant difference between the first two was due to the difference in water stress levels. On the other hand, the difference in leaf number between plants treated with NP-LWS and LP-SWS could be due to low phosphorus and severe water stresses (drought). Similarly, research results reported in soybean (Fredeen et al., 1989) and cotton (Singh et al., 2006) revealed that phosphorus deficiency had some effect on the rate of leaf emergence.

Plants of chickpea accessions subjected to different treatments showed little difference in height at the first and second sampling days (28 and 42 DAP). The differences become more visible as the duration of water stress prolonged (56 DAP). Plant height has been reported to be sensitive to water stress in cowpea (Masresha Fetene, 1985), black bean (Nielsen and Nelson, 1998) and chickpea (Yonas Feleke, 1999) and to phosphorus deficiency in field pea (Asgidom Yemane and Skjelvag, 2003) and cotton (Singh et al., 2006). However, in the present study, differences in plant height under the different treatments in each accession were insignificant and inconsistent probably due to the superimposition of other stress factors in the greenhouse.

Total leaf area response of three chickpea accessions to water stress and phosphorus deficiency as observed in the present study (Fig.1), is in agreement with those described by Fredeen et al. (1989), Rao and Terry (1989), Thomas and Fukai (1995), Nielsen and Nelson (1998), Yonas Feleke (1999) and Jensen et al. (2002) in different crop species. In this study, the trend for the reduction in total leaf area was towards the low phosphorus treatments, the water stress levels remained the same. This is not to say that differences were not observed across water stress levels in the normal phosphorus treatments. Several research results, such as Masresha Fetene (1985) in cowpea, Thomas and Fukai (1995) and Yonas Feleke (1999) in chickpea and Nielsen and Nelson (1998) in black bean reported that water deficit stress severely inhibited leaf area expansion through its effect on pressure potential (turgor). Besides this, Fredeen et al. (1989) in soybean, Rao and Terry (1989) in sugar beet and Jensen et al. (2002) in white clover investigated that phosphorus deficiency decreased leaf expansion into two ways. First, by decreasing the hydraulic conductance of the root leading to reduced water transport and thus the turgor necessary for leaf cell enlargement. Second, through the effect of low level of phosphate for the expansion of epidermal cells, where leaf epidermal cell expansion appears to be a critical process in the expansion of leaf blade and phosphate being required for some important but unknown role in leaf epidermal expansion. Similarly, in the present study, total leaf area under LP-LWS, LP-MWS and LP-SWS treated plants was lower than the corresponding NP-LWS, NP-MWS and NP-SWS ones. And thus, there were a 39, 22 and 8% decrease in plants of accession Yaya Gulele and 27, 9 and 16% decrease in plants of accession Legambo. It was also lower by 21, 12 and 13% in plants of accession Moretena Jiru under LP-LWS, LP-MWS and LP-SWS treatments, respectively. In addition, chickpea plants shed the oldest leaves after 7 days of water stress, which is similar to the one reported by Tilahun Amede and Schubert (2003). The sum total of all these (decreased leaf expansion and shedding of older leaves) reduced total leaf area in water stressed and phosphorus deficient chickpea plants.

In general, accession Yaya Gulele had the highest total leaf area in NP-LWS plants, while accession Moretena Jiru attained the lowest in LP-SWS plants. The reduction in total leaf area provided an adaptive mechanism in reducing water losses (transpiration) from the major transpiring surfaces (leaves). This could be taken as a drought avoidance mechanism.

The relative growth rate (RGR) of chickpea accessions was generally established by successive harvests, 42 and 56 DAP, from a population, which has been grown under greenhouse conditions. In the present study, the highest RGR of the leaf was recorded in chickpea plants of accessions Legambo and Moretena Jiru grown under NP-LWS conditions. Stem and root relative growth rates were highest in those chickpea plants of accession Yaya Gulele grown under NP-MWS and low phosphorus treatments (LP-LWS and LP-MWS), respectively. Therefore, relatively better RGR of shoot was observed under normal phosphorus treatments in the three accessions. This showed that chickpea plants partitioned most of the assimilates to the shoot due to the fact that normal phosphorus concentration in the soil, as described by Singh et al. (2006) in cotton improves water relations of plants under water deficit stress. In contrast, the relative growth rate of the root was higher in the low phosphorus treatments in all accessions. This agrees with research results of Fredeen et al. (1989) on soybean and Jensen et al. (2002) on white clover under phosphorus deficiency and Busso et al. (1998) on *Medicago minima* and *Erodium cicutarium* under water stress. Under conditions of water stress and phosphorus deficiency, plants divert most of the photosynthate towards the root, because less of the photosynthates were used in shoot growth due to the above stress factors and the root was the least moisture stressed as compared to the shoot. In addition, root respiration and N_2-fixation were lower at low phosphorus supply. Thus, the assimilates partitioned to the root system were mainly used to increase the size of the root system so as to extract water and nutrients from wider and deeper areas in the soil. On the other hand, the pattern of fine root relative growth rate was inconsistent.

In the present study, chickpea accessions under low phosphorus treatments exhibited lower shoot dry matter production than those grown under normal phosphorus, the water stress levels being the same. Accordingly, chickpea plants of accessions Legambo and Moretena Jiru grown under NP-LWS conditions produced the highest leaf and stem dry weight, respectively, while the lowest dry weight of the leaf was produced by chickpea plants of accession Legambo under LP-LWS and accession Moretena Jiru under LP-SWS. Chickpea plants of accessions Yaya Gulele and Moretena Jiru under LP-SWS produced the lowest stem dry weight. However, the differences were not statistically significant. The reduction in shoot dry weight under low phosphorus treatments was attributed to the lower total leaf area that affects light interception. Tilahun Amede and Schubert (2003), Thomas and Fukai (1995) and Yonas Feleke (1999) in chickpea, Masresha Fetene (1985) in cowpea and Busso et al. (1998) in *Medicago minima* and *Erodium cicutarium* under water stress and Rao and Terry (1989) in sugar beet under phosphorus deficiency reported similar results.

In contrast, root biomass increased in those chickpea plants grown under low phosphorus conditions except in chickpea plants of accession Moretena Jiru. For example, 56 DAP, chickpea plants of accession Yaya Gulele treated with LP-MWS produced the highest root dry weight and plants of accession Legambo grown under NP-LWS produced the lowest. However, in accession Moretena Jiru, root biomass decreased in those plants grown under low phosphorus conditions. This could be an indication that root characters are not the means to overcome stress factors in plants of accession Moretena Jiru. Different from other accessions, Plants of accession Moretena Jiru grown under NP-MWS and LP-MWS had significantly higher root dry weight than those grown under LP-SWS conditions. Finally, fine root dry weight was higher for those chickpea plants grown under normal phosphorus treatments, which is in contrast to the source-sink theory of resource allocation, a theory which states that plants grown under nutrient deficient soils allocate most of their assimilates to the root to enhance root growth (Maycock and Condon, 2000) and in line with the available water in the soil.

An increased root/shoot ratio response was observed in phosphorus deficient plants of accessions Yaya Gulele and Legambo. From all treatments in all accessions, the highest root/shoot ratio was recorded in chickpea plants of accession Yaya Gulele grown under LP-LWS and LP-SWS treatments followed by chickpea plants of accession Legambo treated with LP-LWS. Plants of accession Moretena Jiru showed the lowest root/shoot ratio under LP-MWS conditions. Root/shoot ratio results of the present study are in contrast to Yonas Feleke (1999) who reported similar root/shoot ratios under different water regimes and in agreement with Masresha Fetene (1985) and Jensen et al. (2002) who reported an increased root/shoot ratio under water stress and phosphorus deficiency in cowpea and white clover, respectively. An increased root growth in plants of accession Yaya Gulele and Legambo at the expense of shoot under water stress and phosphorus deficiency can be taken as an adaptive mechanism, which facilitates absorption of available moisture and nutrients in the soil.

5.2. Water relations

Relative water content (RWC) is a method that has recently gained increasing importance over leaf water potential (LWP) as a very relevant physiological measure of plant water deficit. Its advantage is that it accounts for the effect of osmotic adjustment in affecting plant water status, as it estimates all form of water (free and bound water). Two plants with the same LWP can have different RWC if they differ for osmotic adjustment. For drought imposed at vegetative stage, chickpea plants of accession Legambo treated with NP-LWS, NP-SWS and NP-SWS had significantly higher midday RWC (leaf samples taken at 12:00 h) than those treated with LP-SWS, LP-MWS and LP-SWS, respectively. Moreover, chickpea plants of accession Moretena Jiru had significantly higher midday RWC (leaf samples taken at 12:00 h) than chickpea plants of accession Legambo under LP-MWS. Chickpea plants of accession Yaya Gulele had significantly higher predawn RWC (leaf samples taken before sun rise) than chickpea plants of accession Moretena Jiru under LP-MWS treatments (Fig. 5). For drought imposed at flowering stage, both predawn and midday RWC were relatively lower than for drought imposed at vegetative stage in all accessions under all treatments. This is probably because in the flowering stage, water stress was induced after the leaves in all treatments attained their full size (developed fully), which in turn increased the amount of water lost through transpiration. There are reports, which indicate that chickpea plants are more sensitive to water stress when imposed at flowering stage (Saxena et al., 1993 and Ashley, 1999). In general, predawn RWC was higher than midday RWC in all accessions under all treatments, perhaps as explained by Tilahun Amede and Schubert (2003) chickpea had no substantial control over transpiration. On the other hand, predawn (leaf samples taken before sun rise) and midday (leaf samples taken at 12:00 h) RWC of chickpea accessions under normal phosphorus treatments were relatively higher both for drought induced at vegetative and flowering stages than the corresponding low phosphorus treatments. This was supported by Singh et al. (2006) in cotton describing that normal level of phosphorus supply improves the water relations of plants under water stress, with greater water content per unit dry weight of leaf. Besides this, normal phosphorus supply increases the uptake of phosphorus from a drying soil, leading to an enhanced supply of inorganic solutes to the cells in growing leaves that again facilitate osmotic adjustment which could delay the decline in RWC (Conroy et al., 1988).

5.3. Chlorophyll a fluorescence

As explained by Tilahun Amede and Schubert (2003), the photosynthetic rate of chickpea recovered to about 85% of the control after an adaptation period of twelve days to drought, which is a level comparable to that of the third day of stress. Besides this, Bjorkman and Powles (1984) reported that in the absence of bright light, the photochemistry of PS II was unaffected even under extreme water stress. For drought induced at vegetative stage, maximum quantum yield (Fv/Fm) measured 56 DAP by plant efficiency analyzer (PEA) showed no significant difference among the different treatments. However, chickpea plants of accession Yaya Gulele grown under NP-SWS had significantly higher maximal quantum yield of PS II (Fv/Fm) than plants of accession Legambo at 10:00 and 12:00 h of the day. For drought induced at flowering stage, significantly greater Fv/Fm ratio was observed in chickpea plants of accession Moretena Jiru treated with normal phosphorus than those treated with low phosphorus at 10:00 and 18:00 h of the day. When the differential Fv/Fm ratio responses of the three chickpea accessions were considered, chickpea plants of accession Yaya Gulele treated with NP-SWS had significantly higher maximal quantum yield than chickpea plants of accession Legambo and Moretena Jiru at 10:00 h of the day. Chickpea plants of accession Legambo had the lowest maximal quantum yield of PS II (Fv/Fm) under all treatments. In other studies, Souza et al. (2004) in cowpea and Yonas Feleke (1999) in chickpea reported the effect of water stress upon the photochemical system, which was revealed by decrease in the maximum quantum yield of PS II accompanied by an increase in the levels of minimum fluorescence.

Effective quantum yield (ΔF/Fm') of PS II showed a decreasing trend under the low phosphorus treatments in all accessions both for drought imposed at vegetative and flowering stage. The lowering of effective quantum yield was not high enough to produce a significant difference between treatments. However, for drought imposed at vegetative stage, chickpea plants of accession Yaya Gulele treated with LP-LWS and LP-SWS had significantly higher effective quantum yield of PS II than chickpea plants of accessions Legambo and Moretena Jiru, respectively at 18:00 h of the day. The observed decrease in ΔF/Fm' of PS II indicate an overexcitation of the photochemical system due to the accumulation of reduced primary electron acceptors, Q_A (Yonas Feleke, 1999 and Souza et al., 2004). When the diurnal courses of Fv/Fm and ΔF/Fm' were considered, a general decline was observed between 12:00 and 14:00h of the day both in the stressed and control chickpea plants, which recovered later in the afternoon. These diurnal decreases revealed the occurrence of dynamic Photoinhibition, which seemed to be effective in protecting the photochemical apparatus from the high risk of photodamage occasioned by the superimposed stresses to which chickpea plants were subjected.

As reported by Masresha Fetene et al., (1997), quantum efficiency is strongly associated with the reduction in photosynthetic ETR. For drought induced at vegetative stage, electron transport rate (ETR) at 10:00 h of the day was significantly lower in those chickpea plants of accession Yaya Gulele treated with LP-SWS than those treated with NP-LWS, NP-MWS, NP-SWS, LP-LWS and LP-MWS. In addition, chickpea plants of accessions Yaya Gulele and Legambo grown under NP-SWS had significantly greater electron transport rate than plants of accession Moretena Jiru at 10:00 h of the day. However, plants of accession Moretena Jiru treated with LP-

SWS had significantly higher electron transport rate than plants of accession Yaya Gulele at 8:00 and 16:00 h of the day. For drought imposed at flowering stage, differences in ETR were inconsistent. In general, the trend showed that water stressed and phosphorus deficient chickpea plants had lower ETR, due to perhaps impairing of NADPH, ATP production and RUBP regeneration. Moreover, phosphorus deficiency resulted in reduction of the amount of phosphorus-containing intermediates of the electron transport chain (Rao and Terry, 1989 and Ripley et al., 2004). In addition, ETR was found to increase around midday, probably due to an increase in photosynthetically active radiation (PAR), since ETR was determined as ΔF/Fm’* PAR*0.5*0.84.

5.4. Yield and yield components

It is obvious from the responses observed for yield and yield components that productivity varies with water and phosphorus levels. In both drought imposed at vegetative and flowering stage, chickpea plants of accession Legambo were able to flower earlier than the other plants of chickpea accessions and thus set relatively higher number of pods, but unable to produce higher number of seeds. For drought imposed at vegetative stage, chickpea plants of accession Legambo treated with NP-LWS had significantly greater number of Pods/plant than those treated with NP-SWS, LP-MWS and LP-SWS. Similarly, chickpea plants of accession Moretena Jiru treated with NP-LWS had significantly greater number of pods/plant than those treated with NP-SWS and LP-SWS. For drought induced at flowering stage, chickpea plants of accession Legambo treated with NP-LWS and LP-LWS had significantly greater number of pods than those treated with NP-SWS, LP-MWS and LP-SWS. Besides, Chickpea plants of accession Legambo treated with NP-MWS had also significantly greater number of pods than those treated with LP-MWS. In other accessions, Chickpea plants of accession Yaya Gulele treated with NP-LWS had significantly greater number of pods/plant than those treated with LP-SWS. Moreover, plants of accession

Legambo grown under NP-LWS, NP-MWS and LP-LWS had significantly greater number of pods at $p < 0.05$ than chickpea plants of accession Moretena Jiru. Plants of accession Legambo treated with LP-LWS had also significantly greater number of pods than plants of accession Yaya Gulele (Table. 5). Yield reduction as observed in the present study due to reduced number of pods was reported in chickpea (Thomas and Fukai, 1995) and (Yonas Feleke, 1999) and black bean (Nielsen and Nelson, 1998) under water stress and in field pea (Asgidom Yemane and Skjelvag, 2003) and cotton (Singh et al., 2006) under phosphorus deficiency by decreasing fruiting branches.

For drought induced at flowering stage, pod weight/plant and seed weight/plant showed significant differences among accessions in addition to pod number/plant. Accordingly, Chickpea plants of accession Yaya Gulele treated with NP-LWS and LP-LWS had significantly higher pod weight/plant than those chickpea plants of accession Legambo and Moretena Jiru, respectively. In contrast, plants of accession Legambo and Moretena Jiru grown under LP-SWS had significantly higher pod weight than plants of accession Yaya Gulele. On the other hand, chickpea plants of accession Yaya Gulele grown under NP-LWS and LP-LWS had significantly higher seed weight/plant than those plants of accession Legambo and Moretena Jiru, respectively (Table. 5). However, these differences were not observed for drought imposed at vegetative stage. In addition, yield and yield components were severely reduced for drought imposed at flowering stage. This is due to the differential sensitivity of developmental phases in pulses to drought. Among the phases of development, vegetative phase is the most drought tolerant and flowering phase is the most sensitive (Ashley, 1999). The sensitivity of flowering phase is due to the large leaf area carried by plants at the end of the vegetative development and the diversion of assimilates from the roots to the developing fruits at the onset of flowering (Fitter and Hay, 1987), an abrupt and progressive increase in transpiration, accompanied by reduction in absorption of both water and minerals from the soil (Ashley, 1999) and lack of new root growth and aging of some of the early formed roots (Saxena, et al., 1993). Moreover, Nayyar et al. (2003) reported that water stress during the reproductive stage in cultivated species of chickpea leads to flower abortion, poor pod set, formation of infertile pods and impaired seed filling. All these significant differences in yield and yield components under the various moisture stressed and phosphorus deficient chickpea plants are results of the low photosynthetic rate which is caused due to lower total leaf area and hence low leaf sucrose concentration that reduce the rate of sucrose export from the leaves to the pods (source limitation) and accumulation of sucrose in flowers and pods which may be partially due to decreased invertase activity (sink limitation) which cleaved sucrose into hexose sugar that provides substrate necessary for pod growth (Liu et al., 2004).

6. SUMMARY AND RECOMMENDATIONS

The results of the present study showed the effects of water stress and phosphorus deficiency on growth and physiology of three chickpea accessions. According to the result of the study, a general decrease in shoot biomass and an increase in root biomass were observed under drought and low phosphorus conditions. However, lower root dry weight was observed in those chickpea plants of accession Moretena Jiru under drought and low phosphorus conditions. The greater root dry weight in chickpea plants of accession Yaya Gulele and Legambo is an adaptive mechanism that creates greater chance of extracting available water and nutrient from the soil. Chickpea plants of accession Legambo flowered earlier and able to set relatively higher numbers of infertile pods. Therefore, under field conditions, this character (earliness) can probably be advantageous. Similarly, reductions in maximal quantum yield (Fv/Fm), effective quantum yield (ΔF/Fm’) and electron transport rate were observed under water and phosphorus stressed chickpea plants where maximal quantum yield (Fv/Fm) and effective quantum yield (ΔF/Fm’) can be still taken as key characters. Accordingly, the results of this study indicated that better root growth, higher leaf RWC and photosynthetic performance in plants of accession Yaya Gulele; better root growth and early maturity in plants of Legambo; lower total leaf area, higher leaf RWC and photosynthetic performance in plants of accession Moretena Jiru could be taken as drought and phosphorus deficiency avoidance mechanisms in plants of these chickpea accessions.

It is recommended that adaptive traits such as better root growth, low total leaf area, early flowering, higher leaf RWC and higher photosynthetic performance could be considered in the selection of these chickpea accessions for cultivation in drought prone and phosphorus deficient areas in Ethiopia. Finally, further research to determine biochemical (osmotic adjustment) responses of these accessions so as to clearly understand and identify drought tolerance and phosphorus acquisition mechanisms is required.

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DECLARATION

I, the undersigned, declare that this Thesis is my own work and all sources of materials have been duly acknowledged.

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