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PREVIEW

**PHYSIOLOGICAL AND DEVELOPMENTAL RESPONSES OF NORMAL
AND DENSE PUBESCENT SOYBEANS [*Glycine max* (L.) Merr.]
TO WATER STRESS**

**By
Gandoul I. Gandoul**

A DISSERTATION

**Presented to the Faculty of
The Graduate College at the University of Nebraska
in Partial Fulfillment of Requirements
for the Degree of Doctor of Philosophy
Major: Agronomy**

**Under the Supervision of Professor Jerry D. Eastin
Lincoln, Nebraska**

August, 1995

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Physiological and Developmental Responses of Dense and Normal Pubescent

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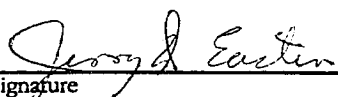
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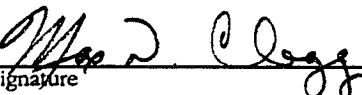
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**PHYSIOLOGICAL AND DEVELOPMENTAL RESPONSES OF NORMAL
AND DENSE PUBESCENT SOYBEANS [*Glycine max* (L.) Merr.]
TO WATER STRESS**

Gandoul I. Gandoul, Ph.D.

University of Nebraska, 1995

Adviser: Jerry D. Eastin

Water and temperature stresses are the most limiting factors for crop production in many dry land production systems. The need to understand and relate responses of essential physiological processes to yield limiting plant developmental processes is important. Experiments were conducted to evaluate soybean responses to water stress in terms of net carbon exchange (NCE), transpiration (TR), respiration (R), assimilate partitioning and growth. Dense (CD) and normal (CN) pubescent Clark soybean isolines were grown under wet and dry conditions. Biomass, leaf area (LA) and leaf area index (LAI), plant height, canopy NCE, canopy and pod R were measured during selected growth stages. Differential responses to water stress in total dry matter production were greatest under dry conditions where the CN isoline produced 10% less total dry matter than the CD. The CD isoline partitioned 20% of its dry matter to reproductive organs compared to 12% for CN. Early in the season when temperatures were high, the CD had 20% higher LAI than the CN. Midday values of NCE were higher for CD isoline than for CN. Similarly, TR and canopy temperature were lower in the CD than in CN. Net carbon exchange was depressed at low soil moisture when vapor pressure deficit (VPD) was more than 3.0 kPa and air temperature (T_a) was 35.5 °C. Low soil moisture, high T_a and VPD resulted in 3 °C higher canopy temperature (T_c) in CN than CD. High T_c probably caused stomatal closure which resulted in decreased NCE.

Respiration rates were higher under wet conditions than dry conditions presumably due to higher carbon assimilation. Under dry conditions the CN isoline had higher respiration

rates than the CD isoline. This may be due to higher maintenance respiration requirements in the CN because of greater water stress. There were no significant differences between the two isolines for pod respiration rates. The proportion of pod respiration to total canopy respiration ranged from 18 to 37% depending on the growth stages and soil moisture content.

Leaf growth and expansion were significantly different between isolines. Dense isolines had higher leaf expansion rates than the normal isolines. Results indicate that the dense pubescent isolines performed better under water and temperature stresses than the normal isolines. Incorporating dense pubescence in other legumes adapted to dry land areas particularly in the semi-arid tropics seems useful.

PREVIEW

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DEDICATION

This dissertation is dedicated to:

My late father: Ibrahim Gandoul who inspired in me the value of education. May peace be upon him.

My mother: Nagiya Mohamed Siddig who instilled in me the discipline and character to persevere and serve humanity. This is a tribute to her motherhood.

My wife: Khalda for her love, daring patience and the hard work she did to earn an education. May God help her.

My son: Ahmed who filled our life with love and all that we needed.

G.I.G

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INTRODUCTION

Environmental stresses such as water, high temperatures and nutrient deficiencies constitute the most limiting factors for plant growth and productivity in many dry land areas (Sionit and Kramer, 1977; Eastin et al., 1983) including the semi-arid tropics (SAT). Water is essentially always limiting and soils are often marginal in water holding capacity. High temperatures are usually limiting some time during the season. Soil nitrogen (N) is usually deficient because soils have often been continuously cropped to cereals without N application. For example, in rainfed mechanized farming in the Gedarif area of Sudan, grain sorghum has been continuously monocropped on the same land for over fifty years without N fertilizer applications. This practice has resulted in low sorghum yields. Strategies to improve cereal production under these conditions can best be based on improvement of both water use efficiency (WUE) and nutrient use efficiency (NUE). Improving either water or fertility usually improves yields and often results in yields greater than the additive water and/or N effects alone (Sanders and Roth, 1985). Commercial N fertilizer often results in increased yields but sometimes causes excessive early growth and water mining to the point that not enough water remains to mature the crop. Another problem is that most farmers in developing countries of the SAT can not afford high inputs of N fertilizers due to limited resources and credit. In the absence of N at affordable prices, the inclusion of legumes in the cropping system may provide a better alternative to enhance cereal yields. In other words if cereal yield is to be improved and stabilized in many SAT areas it will be necessary to improve production and use of N fixing legumes. The major advantage of including legumes in cropping systems is that they increase soil N level and recycle other nutrient elements. The effects of legumes in rotation are complex and are hard to define accurately but advantages include recycling of nutrients, improved organic matter, slow nutrient release from organic matter, improved water infiltration to reduce runoff and better pest control. In

the Gezira (Sudan), a SAT area, legumes in rotation contributed an equivalent of 170 kg N ha⁻¹ (Musa, 1973) and 100 kg N ha⁻¹ (Mohamed, 1994) when grown in rotation with sorghum. The average yield increase was 50% compared to continuous non fertilized sorghum (Mohamed, 1994). Considering water and nutrient limitations, and the substantive but ill defined contributions of legumes in cereal based rotation to soil N and other soil characteristics, it is obvious that a greater understanding of legume role and performance in the SAT is desirable. Improving legume adaptability to achieve acceptable growth under dry conditions is a reasonable approach in securing and maximizing the advantages of legumes to increase yield from improved WUE and NUE of subsequent cereal crops. Since canopy NCE, transpiration (TR), assimilate partitioning and respiration (R) are essential physiological processes contributing to final yield, it is assumed valuable to know how they are influenced by environmental stresses. Understanding the variable plant responses of these processes under water stress may aid in identifying which processes contribute most to stress resistance and which genotypes have the best stress resistance. Photosynthesis is of interest because (i) it is sensitive to water stress (Hsiao, 1973) and (ii) it is a determinant of dry matter production and accumulation (Murata, 1981). Simultaneous measurement of photosynthesis and TR gives an estimate of instantaneous water use efficiency (IWUE). Respiration provides the energy transfer required to drive most dark syntheses (amino acid, carbohydrate, protein, oil, etc) in different sinks. The ultimate objective is to identify stress resistant legumes which can be integrated into cereal based cropping systems under dry environments. The specific objectives were to evaluate the influence of pubescence levels in soybean isolines on (1) net carbon exchange, transpiration, respiration and agronomic responses under water stress at different growth stages, (2) on partitioning of assimilates between various sinks and (3) on leaf growth as a sensitive stress indicator.

During the course of this study, experiments were conducted under field conditions during 1991 and 1992; and under greenhouse conditions during 1993. This dissertation is presented in three chapters. The first chapter provides physiological responses of contrasting soybean genotypes to stress at different growth stages with emphasis on dry matter partitioning, NCE and water vapor exchange. Chapter 2 characterizes the response of canopy and pod respiration. Chapter 3 details differential water stress responses of soybean isolines for total leaf water potential, CO_2 and water vapor exchange and leaf growth.

PREVIEW

REVIEW OF LITERATURE

IMPORTANCE OF LEGUMES IN ROTATION

Legumes can provide substantial amounts of biologically fixed N to the succeeding cereal crops. The amount of N contributed by legumes has been compared with an N rate at which equivalent yields have been obtained following a non-legume crop depending on environmental conditions. In a series of legume/cereal rotation studies in Eastern Nebraska soybean preceding pearl millet resulted in a 45 Kg N ha⁻¹ credit to pearl millet (Mohamed and Clegg, 1993), and 76 kg N ha⁻¹ to grain sorghum (Clegg, 1982). In Sudan, Phillipessara [*Phasulus trilobus* (Ait.)] and Clitoria [*Clitoria ternata* (L.)] fixed the equivalent of 111 and 90 kg N ha⁻¹, respectively (Mohamed, 1994). This resulted in an average of 50% increase in sorghum yield over continuous unfertilized sorghum plots. Clegg (1982) reported a 43% increase in grain sorghum yield following soybean compared to continuous unfertilized sorghum. In Botswana, Africa, grain sorghum yield increases were 48 and 54% following cowpea and peanuts, respectively (Gakale, 1986). asimilar results were obtained in the central clay plains of the Sudan. All these authors attributed the response of sorghum to crop rotation with legumes as primarily a N response. While these studies indicate that yield increases were due to the N supply, other studies demonstrate that the yield increases were due to other "rotation effects" such as enhancement of soil physical properties (Odell et al., 1984). Crop rotations tend to increase soil organic matter. Organic matter improves soil structure, nutrient supply, creates better water infiltration and aeration (Power and Doran, 1989). The concentration of crop residues and organic matter in the soil increase the diversity and population of microorganisms, which can result in greater recycling not only of N within the soil but also lessens leaching of plant-available N (Power and Doran, 1989). Even though the effects of rotation on NUE are difficult to establish, Abshahi et al. (1984) reported on NUE for N fertilizer and legumes in corn.

PHOTOSYNTHESIS AND YIELD RELATIONSHIPS

The hypothesis that increased photosynthetic rates is necessary for high yield is still popular (Coombs, 1984). Direct and indirect evidence supporting this hypothesis includes increased seed yield from CO₂-enriched environment around the canopy (Campbell et al, 1990; Chen and Sung, 1990 Bunce, 1992) and from adding supplemental light to the lower canopy positions (Bunce, 1992). Studies using single leaf photosynthesis and net assimilation rates also support the concept of yield enhancement through improved photosynthetic performance (Buttery et al., 1981). According to these authors genotypes selected for high yields tend to have high photosynthetic rates. Buttery et al. (1981) reported a positive correlation between leaf photosynthesis and seed yield in 12 maturity group II cultivars during the reproductive period. Srinivasan et al. (1985) found a significant positive correlation between leaf photosynthesis and total dry matter and pod development stage in green gram [*Vigna radiata* (L.) Wilczek]. However, evidence to the contrary exists (Harrison et al., 1981; Boerma and Ashley, 1988). The disagreement in these findings is because most studies evaluating leaf photosynthesis have not measured seed yield. Zelitch (1982) stated that the lack of a positive relationship between photosynthesis and production in most studies is due to instantaneous measurements of photosynthesis at a single period of development rather than seasonal measurements.

ENVIRONMENTAL FACTORS INFLUENCING PHOTOSYNTHESIS

1. WATER STRESS

The effects of water stress on photosynthesis have been well documented (Boyer, 1976; Hsiao, 1973; Amthor and McCree, 1990; Osmond, et al., 1980). Moisture stress inhibits photosynthesis, and depending on severity of the stress, substantial decreases in photosynthetic rates occur. The inhibition of photosynthesis by water stress is attributed to stomatal and non-stomatal components or to the combination of the two (Farquhar and

Sharkey, 1982). In the first case the response of photosynthesis to water stress is mediated by impeded CO_2 supply following stomatal closure and indirectly by effects of dehydration on the photosynthetic system and loss of turgor in guard cells (Amthor and McCree, 1990). The depression of photosynthesis can be exclusively ascribed to stomatal closure and the consequent isolation from external CO_2 supply (Osmond et al., 1980). Two theories explain the cause of stomatal closure with the occurrence of water stress (Boyer, 1976). The most accepted one is that the guard cells lose turgor as a result of decline in leaf water potential. The second theory is based on reduced chloroplast activity associated with leaf water potential at which time stomatal closure occurs.

Non-stomatal factors such as increased resistance of the mesophyll to CO_2 diffusion, reduced activity of enzymes in chloroplast, inhibition of electron transport of photosystem II and photophosphorylation are involved in the reduction of photosynthesis. However, when water stress develops slowly, photosynthesis declines due to a simultaneous decline in stomatal and nonstomatal properties (eg. low stomatal and mesophyll resistances).

2. TEMPERATURE

Temperature effects on plant physiological processes vary widely among plant species and even amongst the several component of biochemical reactions of single broad processes such as photosynthesis or R. The deactivation of enzymes is one cause of the inhibition of photosynthesis at high temperatures. The photosynthetic capacity are reversible, the functional process reaction groups which may limit Ps by high temperature include photobiochemistry, enzymes of carbon assimilation, photorespiration and utilization of assimilates (Kozba and Edwards, 1987; Nie et al., 1992). The most likely inhibitory effects of high temperature on photosynthesis in C_3 plants are due to a stimulation of photorespiration. According to Kozba and Edwards (1987), apart from limitations imposed by photorespiration, photosynthesis was limited by the rate of triose utilization at suboptimal

temperatures and by substrate availability at optimal temperatures. Nie et al. (1992) suggested that the effects of temperature on maize Ps could be explained by effects on CO₂ diffusive resistance and photorespiration. These authors attributed decreased photosynthetic rates to increased stomatal limitation to CO₂ uptake.

PLANT FACTORS INFLUENCING PHOTOSYNTHESIS

Leaf pubescence

Leaf hairs provide a morphological means by which plants interact differently with their environment. Baldocchi et al. (1983) indicated that a soybean canopy with densely pubescent leaves had a significant lower flux of latent heat and a significantly higher flux of sensible heat. This differential partitioning of net radiation into latent and sensible heat was also accompanied by a reflective scattering of solar radiation into the canopy. The deep penetration of radiation into the canopy of dense pubescent isolines improved canopy photosynthesis (Lemuer and Rosenberg, 1975; Nielsen et al., 1984) and improved WUE by reducing evapotranspiration (ET) and by increasing photosynthesis.

With respect to high temperature and water stress conditions, the presence of leaf hairs is thought to modify leaf properties and physiological processes (Baldocchi et al., 1983; Nielsen et al., 1984). Modification of canopy micro-environment such as boundary layer may directly influence both Ps and TR through its influence on the diffusion of carbon dioxide into and water out of the leaf surface and also the rate of heat transfer to the leaf (Clawson, 1983; Baldocchi et al., 1983).

EFFECTS OF LEAF PUBESCENCE ON TRANSPIRATION AND WATER USE EFFICIENCY

According to Wooley (1964) densely pubescent soybeans have a higher boundary layer resistance to water vapor loss. Clawson (1986a, b), using soil water balance methods, confirmed that the dense isolines had less TR and better WUE. Clawson (1983) reported

that leaf pubescence decreased stomatal frequency by 10% in dense pubescent Harosoy cultivar compared to its normal near-isoline. Decreased stomatal frequency increased stomatal resistance to water vapor and decreased TR. Hairiness decreased wind speed by about 40% at the leaf surface thus increasing boundary layer resistance which would decrease TR rates (Wooley, 1964). Garay and Wilhelm (1983) reported that the dense pubescent Harosoy isoline had greater root density, extended deeper into the soil. Consequently it was effective in extracting the total soil water which is a critical water stress avoidance mechanism during prolonged period of drought.

EFFECTS OF LEAF PUBESCENCE ON GROWTH AND YIELD

Soybean vigor, growth and grain yield are all affected by morphological variation in pubescence density (Clawson et al., 1986; Specht, 1985; Baldocchi et al., 1983; Zhang et al., 1992). Agronomic trials showed consistent observations that the dense pubescent isolines matured later, were taller, had higher incidence of lodging and had larger seed size (Specht et al., 1985; Zhang et al., 1992). These differences raise questions as to how isogenic these isolines are. Growth analysis studies have demonstrated that a final difference in plant height is not the result of a delay in senescence rather the accumulation of a season-long advantage of dry matter accumulation rates (Clawson et al., 1986a). Singh et al. (1971) observed that dense pubescence in soybeans led to greater plant height.

RESPIRATION

Respiration can be divided into two major components, growth and maintenance R (McCree and van Bavel, 1978). Growth R supplies energy for synthesis of new plant materials (McCree, 1974). In actively growing plants, growth R represents the major respiratory component and can be slowed by environmental conditions.

Maintenance R supplies energy for the maintenance processes which require a continuous input of energy (Biscoe and Gallagher, 1977; McCree and van Bavel, 1978).