UNIVERSITI PUTRA MALAYSIA

REPRODUCTIVE ALLOMETRY AND PLASTICITY IN RELATION TO PLANT POPULATION DENSITY IN SOYBEAN [(Glycine max L.) Merrill.]

HASSAN HAMAD HASSAN EL-ZEADANI

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By

HASSAN HAMAD HASSAN EL-ZEADANI

Thesis Submitted to the School of Graduate Studies, Universiti Putra Malaysia, in Fulfilment of the Requirements for the Degree of Doctor of Philosophy

March 2015

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DEDICATION

TO WHOM IN WHICH THEIR TRUE LOVE AND SUPPORT WERE BEHIND MY SUCCESS

TO MY MOTHER AND TO THE MEMORY OF MY FATHER

Abstract of thesis presented to the Senate of Universiti Putra Malaysia in fulfilment of the requirement for the degree of Doctor of Philosophy

REPRODUCTIVE ALLOMETRY AND PLASTICITY IN RELATION TO PLANT POPULATION DENSITY IN SOYBEAN [(*Glycine max* L.) Merrill.]

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March 2015

Chairperson: Associate Professor Adam Puteh, PhD
Faculty: Agriculture

The vegetative and reproductive stages during plant growth are strongly interdependent and ultimately influence the potential yield. The biomass produced by plant during the early part of its life cycle are eventually allocated to various vegetative and reproductive structures and functional plant processes. From an agronomic perspective, biomass quantification to different plant organs especially to the economic yield based on allometric and plasticity analyses are limited. Thus, the general objective of this study was to evaluate the use of allometry and plasticity approaches in comparing several soybean varieties in relation to changes in plant population densities especially under the tropical growing environment. The specific objectives were: (i) to determine the effect of plant population density of selected vegetable- and grain-type varieties of soybean on changes of growth rates and seed fill duration at specific reproductive growth stages and the relationships of individual seed growth rate (SGR*i*) and seed filling period (SFP) with yield components, (ii) toquantify allometric changes based on relative growth rate of leaf and seed mass, and source-sink relationship due to plant population pressures at specific reproductive growth stages, and (iii) to determine yield plasticity responses to plant density variations based on individual plant and per area basis, and the use of plasticity for designing the optimal field planting density. In the first experiment (2010), three soybean varieties [AGS 190 (vegetable-type), Palmetto and Deing (grain-types)] were grown at 20, 30, and 40 plants m^{-2}. The second experiment (2011), AGS190 and grain-types of Argomolio and Willis were grown at 20, 30, and 50 plants m^{-2}. At 20, 30, and 40 or 50plants m^{-2} are considered as low (L), normal (N), and high planting density (H), respectively. The field experimental design in both years was randomized complete block design (RCBD) with three replications.

Plant density did not affect the SGR*i* or SFP, but they differ among varieties during different reproductive growth stages. Dry matter accumulation in the seed was highest during reproductive growth stages from full size seed to physiological maturity stage (R6 to R7, respectively). This period of seed growth and development

had the highest SGRi and SFP. Increased plant density had decreased seed number of individual plant. Seed number per plant adjustments indicated the stability of individual final seed size within variety that was insensitive to the changes in plant density. Both SGRi and SFP were correlated negatively with seed number per plant and positively with final seed size. In this study (under humid tropical growing conditions) the selected vegetable- and grain-type soybeans could be grown successfully even with maximum daily temperature > 32˚C, and the seed number, seed weight per plant, and number of plants per area were important features to determine yield potential.

The source-sink relationship of leaf and seed mass per plant with the consideration of time were analyzed allometrically by taking the ratio of respective relative growth rate of leaves (RGR_l) to seeds (RGR_s) with a model of $\alpha = \frac{\mathrm{RGR}l}{\mathrm{RGR}s}$, where α = allometry. The derived 'α' values explain three types of biomass allocation to seeds. At α > 0 allometry zone, the leaves daily current photoassimilate was used for further leaf growth while partitioning some for seed development. When at α = 0 zone, it was a point in which all current photoassimilate in green leaves was partitioned to seed development, and it corresponds to the beginning of linear phase of seed growth. It occurred at the beginning of R6 for vegetable-type of AGS190 and the beginning of R5 for the grain-types of Deing, Palmetto, Argomolio, and Willis. In the zone of α < 0, the leaves begin to senesce and the increase in seed size that primarily due to mobilization current and stored assimilates from vegetative organs and also current photosynthetic produced by the green tissues of reproductive organ.

Related to allometry analysis, the beginning of the effective seed filling period (ESFP) was determined based on the intersection point of the proportionate leaf RGR and seed mass to their respective predicted maximum values that produced by the curves of $RGR = b + 2ct \; and \;\; y = e^{(a+\mathrm{b}t+ct^2)}$, respectively. The resultant was $\int(b + 2ct)^* dt - \int\left(e^{a+\mathrm{b}t+ct^2}\right)^* dt = 0$, where '*' indicates the predicted values of the leaf RGR and seed mass that firstly converted to their proportionate values based on their maximum predicted values, and t is days after planting. The ESFP that generated in this study is an alternative to effective filling period (EFP) method with an additional feature that simultaneously includes vegetative and reproductive growth consideration. The method of ESFP was found quantitatively and physiologically reliable in the five tested soybean varieties for two growing seasons. Average overall densities, the ESFP and EFP for all varieties studied were shorter or similar to the duration of morphological stages of beginning seed (R5) to physiological maturity (R7).

Plasticity based on per plant and per area basis were indexed as *pt* and *Pt*, respectively. Varieties tested showed high plasticity (*pt*) in seed number per plant for density setting of L-H than that of L-N where L, N, and H were the low, normal, and high densities, respectively. This result indicated that seed number per plant was gradually reduced with increasing plant density. Genetically, the range of plasticity was slightly less for the large seeded vegetable-type variety (AGS190) than those of the small seeded grain-type varieties (Argomolio, Palmetto, Willis and Deing) grown in Malaysia tropical conditions. The plasticity of seed number based on per area basis (*Pt*) was predicted by new model $Pt = -[(1 + \mathrm{bn} + 2cn^2)e^{(a+\mathrm{bn}+cn^2)}]$. There were three types of plasticity in seed m^{-2} across plant densities pressure; positive, negative and no phenotypic plasticities. The curve that started with a positive plasticity with increasing plant density had optimum planting density related design at its lower density (20 plants m^{-2}) which was observed in AGS190 and Willis. A trend that started with a negative plasticity with increasing density, the optimal planting density occurred when $Pt = 0$. At this plasticity, the estimated optimum planting densities for Deing, Palmetto, and Argomolio ranged between22 - 29 plants m^{-2} to achieve maximum seed number m^{-2}. The optimum yield per area occurred at low to normal density range. Per area plasticity is more practical than the per plant basis plasticity when describing the maximum yield for the designing of planting densities in soybean cultivation in tropical environments.

The study had successfully used the allometry and plasticity in describing the agronomic and physiological indicators in growing soybean under the tropical condition. The physiologists, breeders and agronomists should exploit on the allometry of RGR of leaves over seeds ($\alpha = 0$), per plant plasticity ($pt= 0$), and per area plasticity ($Pt = 0$ or the first appearing of *Pt* when *Pt* start with positive value in *Pt* versus density curve), respectively in developing and expending soybean varieties that could be successfully grown under humid tropical environments.

Abstrak tesis yang dikemukakan kepada Senat Universiti Putra Malaysia sebagai memenuhi keperluan untuk ijazah Doktor Falsafah

REPRODUKTIF ALLOMETRI DAN PLASTISITI BERHUBUNG DENGAN KEPADATAN POPULASI TUMBUHAN DALAM KACANG SOYA [(*Glycine max* L.) Merrill.]

Oleh

HASSAN HAMAD HASSAN EL-ZEADANI

Mac 2015

Pengerusi: Profesor Madya Adam Puteh, PhD
Fakulti: Pertanian

Peringkat vegetative dan pembiakan semasa pertumbuhan tumbuhan adalah saling bergantung yang akhirnya mempengaruhi potensi hasil. Tumbuhan menghasilkan biomass semasa permulaan kitaran hayatnya, yang akhirnya biomas tersebut diperuntukkan kepada pelbagai struktur vegetatif dan pembiakan dan fungsi proses tumbuhan. Dari perspektif agronomi, kuantifikasi biomass kepada organ-organ tumbuhan yang berbeza terutama kepada hasil ekonomi berdasarkan analisis allometri dan plastisiti adalah terhad. Oleh itu, objektif umum kajian ini adalah untuk menentukan penggunaan pendekatan "allometri dan keplastikan" dalam menilai beberapa varieti kacang soya dalam persekitaran tropika. Objektif khusus adalah, (i) untuk menentukan kesan kepadatan populasi tumbuhan pada kadar perubahan dan tempoh tumbesaran di peringkat tumbesaranbiji benih, dan hubungan kadar pertumbuhan benih (SGRi) dan tempoh pengisian benih (SFP) keatas komponen hasil dan hasil, (ii) untuk menilai pendekatan fisiologi kuantitatif dalam perubahan allometri berdasarkan kadar pertumbuhan relatif antaradaun dan berat biji sepokok serta hubungan sumber-sinkidan tekanan populasi tumbuhan pada peringkat reproduktif, dan (iii) untuk menentukan variasi keplastikan hasil pada kepadatan tanaman berdasarkan response sepokok dan per unit kawasan, dan penggunaan keplastikan untuk rekabentuk kepadatan penanaman yang optimum. Dalam kajian pertama (2010), tiga varieti kacang soya [AGS 190 (jenissayuran), Palmetto dan Deing (jenisbijirin)] ditanam pada 20, 30, dan 40 pokok m^{-2}. Eksperimen kedua (2011) menggunakan AGS190 dan jenisbijirin Argomolio dan Willis yang ditanam pada 20, 30, 50 pokok m^{-2}. Reka bentuk eksperimen dilapangan dalam kedua-dua tahun ialah rekabentuk blok lengkap terawak (RCBD) dengan tiga replikasi.

Kepadatan tanaman tidak menjejaskan SGRi atau SFP, tetapi ia berbeza antara varietisemasa peringkat pertumbuhan pembiakan yang berlainan. Pengumpulan bahan kering di dalam benih adalah paling tinggi semasa peringkat pertumbuhan pembiakan masing-masing dari R6 ke peringkat R7. Ini tempoh pertumbuhan biji

dan mempunyai SGRi dan SFP tertinggi. Peningkatan kepadatan tanaman telah menurunkan bilangan benih sepokok. Pelarasan bilangan biji per pokok menunjukkan kestabilan saiz individu biji untuk setiap varieti yang tidak peka kepada perubahan kepadatan tanaman. Kedua-dua SGR dan SFP telah berkorelasi negatif dengan bilangan biji bagi setiap tumbuhan dan positif dengan saiz benih akhir. Dalam kajian ini di bawah keadaan lembap pertumbuhan tropika, tanaman pilihan dan jenis bijirin kacang soya boleh ditanam berjaya walaupun dengan suhu maksimum harian > 32 ˚C, dan jumlah biji, berat biji sepokok, dan jumlah biji per kawasan adalah ciri-ciri penting untuk menentukan potensi hasil.

Hubungan sumber-sinki daun dan berat biji per pokok dengan masa dianalisis secara allometri dengan mengambil nisbah kadar pertumbuhan relatif diantara daun *(RGR_l)* dan benih *(RGR_s)* dengan model $\alpha = \frac{\mathrm{RGR}l}{\mathrm{RGR}s}$, di mana α = allometri. Nilai 'α' menerangkan tiga jenis peruntukan biojisim untuk perkembangan biji. Pada α > 0 zon allometri ini, hasil fotoasimilasi daun harian semasa adalah digunakan untuk penerusan pertumbuhan daun manakala pembahagian beberapa untuk perkembangan biji. Pada α = 0 zon adalah titik di mana semua fotoasimilasi semasa dalam daun hijau dibahagikan untuk perkembanganbiji, dan ia sepadan dengan permulaan fasa linear pertumbuhan biji. Ia berlaku pada awal R6 untuk AGS190 dan pada awal R5 untuk jenis-bijirin Deing, Palmetto, Argomolio dan Willis. Pada zon α < 0, daun mula senesce dan peningkatan saiz biji adalah terutamanya disebabkan oleh mobilisasi semasa dan tersimpan daripada organ-organ vegetatif dan juga fotosintesis terkiniyang dihasilkan daripada tisu hijau organ pembiakan (buah).

Berdasarkan daripada analisis allometri, permulaan tempoh pengisian biji efektif (ESFP) dapat ditentukan berdasarkan titik persilangan keluk RGR daun berkadar dan jisim biji yang disesuaikan dari pada data diramalkan oleh $RGR = b + 2ct \ dan \ \ y = e^{(a+\mathrm{bt}+ct^2)}$, masing-masing. Ini telah menghasilkan $\int(b + 2ct)^* dt - \int\left(e^{a+\mathrm{bt}+ct^2}\right)^* dt = 0$, di mana '*' menunjukkan nilai-nilai yang diramalkan daripada RGR daun dan jisim biji yang kemudiannya ditukar kepada nilai-nilai yang diseragamkan berdasarkan nilai-nilai maksimum yang diramalkan. Kaedah ESFP yang dihasilkan dalam kajian ini adalah alternatif untuk kaedah EFP dengan taktor tambahan yang pada masa yang sama termasuk vegetatif dan pertumbuhan reproduktif.Kaedah ESFP ditemukan secara kuantitatif dan fisiologi yang sesuai dalam lima varieti kacang soya yang diuji selama dua musim. ESFP dan EFP untuk semua varieti yang diteliti adalah lebih pendek atau sama dengan tempoh fasa morfologi R5 ke R7.

Plastisiti berdasarkan kepada basis sepokok dan seunit kawasan adalah masing-masing, diindeks sebagai *pt* dan *Pt*. Varieti yang diuji menunjukkan plastisitas tinggi (*pt*) dalam jumlah biji sepokok untuk pengaturan kepadatan L-H daripada L-N di mana L, N, dan H adalah masing-masing, pada kepadatan tendah, normal, dan tinggi. Ini menunjukkan bahwa jumlah biji sepokok secara bertahap telah dikurangi dengan peningkatan kepadatan tanaman. Secara genetik, julat keplastikan adalah sedikit rendah untuk soya jenis sayuran berbiji besar (AGS190) dibandingkan variti jenis bijiran yang berbiji kecil (Argomolio, Palmetto, Willis dan Deing). Plastisiti jumlah biji berdasarkan seunit kawasan dapat dikira berdasarkan $Pt = -[(1 + \mathrm{bn} + 2cn^2)e^{(a+\mathrm{bn}+cn^2)}]$. Terdapat tiga jenis Plastisiti bilangan dalam biji m^{-2} di pelbagai kepadatan tanaman ; positif, negatif dan tidak plastisiti fenotip.Keluk yang bermula dengan keplastikan positif dan dengan peningkatan kepadatan tanaman mempunyai rekabentuk yang berkait dengan kepadatan penanaman optimum ia itu pada kepadatan rendah (20 pokok m^{-2}), seperti yang di tunjukan oleh AGS190 dan Willis. Trend yang bermula dengan plastisiti negatif dan dengan meningkatkan kepadatan, kepadatan tanaman optimum berlaku apabila Pt = 0 Pada plastisiti ini, anggaran jarak tanaman optimum untuk Deing, Palmetto, dan Argomolio adalah antara 22-29 pokok m^{-2} untuk mendapatkan bilangan biji per m^{-2} yang maksimum. Hasil optimum diperoleh pada julat kepadatan rendah ke normal. Plastisiti berdasarkan unit kawasan adalah lebih praktikal dibandingkan dengan hasil per pokok adalam mereka bentuk jarak tanaman dalam penanaman kacang soya di persekitaran tropika.

Kajian ini telah berjaya menggunakan allometri dan plastisiti dalam menggunakan petunjuk agronomi dan fisiologi dalam penanama kacang soya di environmen tropika. Fisiologis, pembiak baka, danagronomis perlu mengeksploitasi allometri daun daripada biji (α = 0) dan keplastikan per pokok (*pt*= 0) dan keplastikan per kawasan (Pt = 0) masing-masing dalam pembangunan dan perkembangan varieti kacang soya yang boleh ditanam dengan berjayg di persekitaran tropika lembap.

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I certify that a Thesis Examination Committee has met on 12 March 2015 to conduct the final examination of Hassan Hamad Hassan El-Zeadani on his thesis entitled "Reproductive Allometry and Plasticity in Relation to Plant Population Density in Soybean [(*Glycine max* L.) Merrill.]" in accordance with the Universities and University Colleges Act 1971 and the Constitution of the Universiti Putra Malaysia [P.U.(A) 106] 15 March 1998. The Committee recommends that the student be awarded the Doctor of Philosophy.

Members of the Thesis Examination Committee were as follows:

Yahya bin Awang, PhD
Associate Professor
Faculty of Agriculture
Universiti Putra Malaysia
(Chairman)

Mohd Ridzwan bin Abd Halim, PhD
Associate Professor
Faculty of Agriculture
Universiti Putra Malaysia
(Internal Examiner)

Christopher Teh Boon Sung, PhD
Senior Lecturer
Faculty of Agriculture
Universiti Putra Malaysia
(Internal Examiner)

Dennis b. Egli, PhD
Professor
University of Kentucky
United States
(External Examiner)

ZULKARNAIN ZAINAL, PhD
Professor and Deputy Dean
School of Graduate Studies
Universiti Putra Malaysia

Date: 17 June 2015

This thesis submitted to the Senate of Universiti Putra Malaysia and has been accepted as fulfilment of the requirement for the degree of Doctor of Philosophy. The members of the Supervisory Committee were as follows:

Adam Puteh, PhD
Associate Professor
Faculty of Agriculture
Universiti Putra Malaysia
(Chairman)

Ahmad B. Selamat, PhD
Associate Professor
Faculty of Agriculture
Universiti Putra Malaysia
(Member)

Zainal Abidin Bin Mior Ahmad, PhD
Associate Professor
Faculty of Agriculture
Universiti Putra Malaysia
(Member)

Muftah M. Shalgam,PhD
Associate Professor
Faculty of Agriculture
Sebha University, Libya
(Member)

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Name of Chairman of Supervisory Committee: Adam Puteh, PhD

PROF. MADYA DR. ADAM PUTEH
Ketua
Jabatan Sains Tanaman
Fakulti Pertanian
Universiti Putra Malaysia
43400 UPM Serdang, Selangor

Signature: ____________________
Name of Member of Supervisory Committee: Ahmad B. Selamat, PhD

Department of Crop Science
Faculty of Agriculture
Universiti Putra M'sia
43400 UPM Serdang
Selangor, MALAYSIA

Signature: ____________________
Name of Member of Supervisory Committee: Zainal Abidin b. M. A., PhD

Signature: ____________________
Name of Member of Supervisory Committee: Muftah M. Shalgam, PhD

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

LIST OF APPENDICES

LIST OF ABBREVIATIONS

CGR	Crop growth rate
d	Day
DAP	Days after planting
DM	Dry matter
EFP	Effective filling period
ESFP	Effective seed filling period
FSS	Final seed size
GR	Growth rate
H	High planting density
L	Low planting density
l	Leaf
LAI	Leaf area index
LDW	Leaf dry weight
LGR	Leaf growth rate
MMD	Malaysia Meteorological Department
N	Normal planting density
PDW	Plant dry weight
PGR	Plant growth rate
pl	Plant
pt	Plasticity based on per plant basis
Pt	Plasticity based on per area basis
s	Seed
SDW	Seed dry weight
SFP	Seed filling period
SGR	Seed growth rate
SGR*i*	Individual seed growth rate
RGR	Relative growth rate
RGR_l	Leaf relative growth rate
RGR*s*	Seed relative growth rate
t	Time
TDM	Total dry matter
TDW	Total dry weight
α	Allometric coefficient

CHAPTER 1

GENERAL INTRODUCTION

Soybean [(*Glycine max L.*) *Merrill.*] serves as one of the most valuable crops in the world, especially among oilseed crops. It accounts for 57% of the total production of oil seed crops in 2012 and, it is the world's most important grain legume in terms of the total output and international trade (SoyStats, 2013). It is like a highly nutritive crop. Its seed contains about 40% protein and 20% oil, and soybean was the source for 68% and 28% of the global vegetable protein and vegetable oil consumption, respectively in 2012 (Hymowitz et al., 1998; SoyStats, 2013). Soybeans are grown in over 35 countries (Röbbelen et al., 1998; Weiss, 1983). They are cultivated for their high protein and oil content, and few varieties with special traits are planted for vegetable usage (Yinbo et al., 1997). Soybean serves as a valuable plant source for food, feed, and industrial applications. The industrial uses include soy flour, soy milk, soy cake, biscuits, enriched cereal flour and other industrial products. Being a legume plant, it is also enriches the soil by fixing atmospheric nitrogen (Rathore, 2000). Due to their ability to fix nitrogen in the soil, soybean helps to improve productivity of other food and cash crops particularly in mixed crops, and rotational farming (Borget, 1992).

There has been an increasing trend in total production of soybean worldwide. The total production in 1950 was 17.0 million metric tonnes, while in 2011 it was 251.5 million metric tonnes, i.e., with an increase of 14.8 times of that in the 1950's (Jones, 2003; SoyStats, 2012). This trend seemed to be similar to the pattern of the world population increase, i.e., the world population in 1950 and 2011 were 2.6 and 7.0 billion, respectively (Population-Statistics, 2014). The major producers of soybean are Brazil, United States of America, Argentina, China, India, Paraguay, and Canada where they produce 31%, 31%, 19%, 5%, 4%, 3% and 2%, respectively of the total world soybeans yield. The respective tonnages are to 83.5, 82.1, 51.5, 12.6,11.5, 7.8, and 4.9 million metric tonnes (SoyStats, 2013). In East Asia, soybean vegetable varieties have become quite popular in China, Japan, Korea, and Indonesia (Oerke and Ecpa, 1994; Shurtleff and Aoyagi, 2009).

High quality seed for planting is a key component of all grain cropping system, and that in a range of field conditions, high quality seeds are needed in ensuring adequate plant population with a reasonable seeding rate (Hasan et al., 2013). Seed quality is the resultant of the integrated effects of the environment during seed production, and the seed exposure condition during harvest, and storage period (Egli et al., 2005). The influence of competition among plants in a population is ubiquitous. It is infrequent to find a plant that has not been affected negatively by its neighbouring plants (Weiner, 1988). The inter- and intra-specific competition that related to density variable among individual plants would cause the reduction in plant growth and/or increase its probability of death (Selamat, 1987).

In general, crop growth is a function of the internal (genotype) and external (environment) growth factors (Amiri and Kakolvand, 2014). These factors ultimately affects yield. Unfavourable growing conditions reduce soybean seed yield (Frederick et al., 2001). By emphasizing on the yield, the changes could occur in the amount of reproductive part and/or the timing of the onset of reproductive initiation. The plant's reproductive photoassimilate allocation might be affected by stresses, such as high plant densities (high competition), too higher or too low air temperature, and drought (Lemoine et al., 2013). In a wider sense, biotic and abiotic factors are affected by plant population density. Therefore, the plant reproductive output are also affected (Frederick et al., 1998; Linkemer et al., 1998). Optimum plant population is a major factor in maximizing yield and yield's profitability. The yield per unit area increases with the increase in plant population density that generally follow the pattern of an asymptotic curve of yield versus planting density, i.e., smaller increases in total yield are obtained at higher densities but above a certain density, the yield becomes constant with increasing density (Doust and Doust, 1990).

Sensitivity of soybean to the environmental condition could also be due to the types of varieties that are grown in specific growing areas. In achieving the maximum soybean yield potential at those specific areas, some field management should be determined for the respective varieties, such as optimum plant population density, planting date, fertilizer requirements, and diseases control practices. Planting and seedling rates are some of the very important agronomic decisions for farmers to increase soybean seed yield. Based on the Malaysian weather conditions (rainfall, temperature, and daylight length), soybean can be planted and produces high yield with proper management and use of suitable varieties (De Bruin and Pedersen, 2008a; Parsaei, 2011).

Plant densities create different canopy- and root-zone microclimates within plant population that may affect plant growing behaviour and some of field management such as harvesting time. In tropical area like Malaysia, planting date is not constrained by water availability and/or soil temperature, but it may be critical for harvesting time that due to the momentum effect of density-dependence microclimate, especially in the reproductive growth stages.

Plants are most affected by stress during pollination, and the dynamic of seed set during the growth stages in plant development (Alqudah et al., 2011). In order to determine what influence a plant during its life cycle, one often needs to know more factor(s) and not than just the end yield or the final dry matter accumulation. Looking at the yield influencing factors, the plant development as dry matter accumulation at different reproductive growth stages over time is useful. To agronomists, plant growth is frequently defined by the parameters related to the changing time such as vegetative and reproductive dry matter increases over time. The comparative value or ratio between the relative growth rates of vegetative and reproductive organs that is yielding 'allometry' could be used in quantifying agronomically and physiologically the dynamic changes of the respective parts during the growth period or progress. The vegetative and reproductive changes in plants grown in different growing environments at certain growth stages could be quantified in term of plasticity. This plasticity is basically the different performances (based on either per plant or per population density) of the plants that are grown under two different growing conditions. Changes occurring along a plant growth trajectory in actual practice can be interpreted by using the concept of allometry and phenotypic plasticity. The allometry could indicate the trend of photoassimilate partitioning from the vegetative to the reproductive parts. However, the proportion of assimilates that can partitioned to different vegetative and reproductive structures allometrically are little being studied. Among breeders, varietal improvement is used to increase crop yield, whereas the plant population density is the main emphasis agronomically for to be used in seeing the 'true' of maximum yield performance of the recommended variety. One of the approaches is therefore, to carry out research in identifying the soybean reproductive allocation behaviour that could be determined by allometrical and plasticity approaches, subjected to plant population density changes of selected varieties (vegetable- and grain-type soybeans) with respect to yield improvement. While the information on soybean seed growth and development is important in achieving higher yield but the reproductive allocation dynamics is still often confusing, especially for agronomists and plant breeders to produce high yielding varieties. Thus, this study was conducted with the following objectives:

General Objective:

To evaluate the use of "allometry and plasticity" approaches in comparing several soybean varieties in relation to changes in plant population densities. The evaluation takes into consideration the selected physiological and agronomical parameters that affecting the dynamics of seed growth and development under tropical growing environment.

Specific Objectives:

1. To determine the effect of plant population density of selected vegetable- and grain-type varieties of soybean on changes of growth rates and seed fill duration at specific reproductive growth stages [beginning pod (R3), full pod (R4), beginning seed (R5), full seed (R6), and beginning physiological maturity (R7)] and the relationships of individual seed growth rate and seed filling period to yield components.

2. To examine the quantitative physiological approaches that are involved in allometric changes based on relative growth rate of both leaf and seed mass with source-sink relationship due to plant population pressures of selected varieties at specific reproductive growth stages.

3. To determine plant density variations on soybean good characteristic of plasticity resistance in yield in the zone of higher seed number based on individual plant and per area basis and the use of plasticity for designing the optimal field planting density.

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