

Full Length Research Paper

Phenotypic plasticity in soybean (*Glycine max* (Merrill)) genotypes with contrasting growth characteristics subjected to planting density stress at different developmental stages

Mebelo MATAA^{1*} and Isaac SICHILIMA²

¹School of Agricultural Sciences, Department of Plant Sciences, University of Zambia, P. O. Box 32379, Lusaka, Zambia.

²Seed Control and Certification Institute, P. O. Box 350199, Chilanga, Zambia.

Received 21 December, 2018; Accepted 11 February, 2019

A study was conducted to determine phenotype plasticity responses in soybean genotypes subjected to plant density stress at different phenological stages. Plants planted at supra optimal population density (500,000 plants per hectare) were thinned to 400,000 population density at 4 developmental stages: V1 (Full expansion of first trifoliolate leaves), V3 (Four nodes with 3 unfolded trifoliate), V6 (Seven nodes, with 6 unfolded-unifoliolate) and R2 (Full bloom with an open flower at the top). The study was conducted in Chilanga, Zambia. Three varieties: Dina, an indeterminate variety and Magoye and Sc Safari determinate varieties were used. A randomized complete block design arranged as a factorial design with two treatments: varieties and thinning stage and four replications were used. Variety had significant effects on days to flowering, biomass, branching, leaf chlorophyll content, plant height, seed weight, and total grain yield. Thinning time influenced number of branches, plant height, above ground biomass and yield. Plant height increased between 32 and 39% for the thinned treatments. Early thinning increased biomass; thinning at the V8 stage increased biomass by 39% compared to the unthinned treatments. Magoye at 2.42 tons/ha had a higher yield, compared to Dina (2.37 tons/ha) and Sc Safari (1.76 tons/ha). Early thinning (T1) reduced yield by 28%. Soybean varieties used in this study exhibited significant vegetative plasticity. Reducing plant density especially in early vegetative phases reduced plant height, increased branching and biomass allocation to vegetative plant parts.

Key words: Biomass, determinate, indeterminate, phenology, vegetative plasticity, yield, yield components.

INTRODUCTION

Although biologists have always been aware that organisms respond differently to different conditions, environmental effects on phenotype were previously regarded as 'noise' obscuring 'true' expression of the

genotype (Sultan, 1992). This led to the overlooking of the much more interesting aspect of plastic response to environmental variation (Sultan, 2003). Phenotypic responses to different environments may include highly

*Corresponding author. E-mail: mebelomataa@yahoo.com.

specific developmental, physiological and reproductive adjustments that enhance function in these environments (Bradshaw, 1965).

Phenotypic plasticity has been described as the ability of a phenotype to be modified by the environment (Bradshaw, 1965). Nicoglou (2015) discussed the historical aspects of evolution of the plasticity concept, outlined emerging debates and the central role of Bradshaw in developing a model to explain the evolution of plasticity. Two forms of plasticity are recognized, morphological and physiological, each with different mechanisms, resource costs and ecological implications (Bradshaw, 1965; Murren et al., 2015). The first form is essentially meristematic in character and involves replacement of existing tissues by new plant parts with different phenotypic characteristics: it appears to represent a high-cost solution to a change in environment (Grime and Mackey, 2002). The second, physiological plasticity, occurs in differentiated tissues and is associated with visually imperceptible changes in properties brought about by reversible sub-cellular rearrangements: here the costs are lower and the response can be much more rapidly achieved than in morphological plasticity (Mooney and Gulman, 1979; Grime and Mackey, 2002; Larsen and Kershaw, 1975). It has been hypothesized that the two forms of plasticity have consistent associations with distinct sets of traits that coincide with particular habitats and ecologies (Grime, 1977; Grime et al., 1986). The importance of genetic inheritance in plant phenotypic responses in adapting to different environments has remained inconclusive and some workers have suggested that developmental processes of the organism itself act in conjunction with environmental influences to produce an integrated, adaptive phenotypes (Schmalshausen, 1986; Sultan, 1992).

Typically cultivated soybean comprises two crop development forms; the determinate types where vegetative and reproductive phases are well defined and do not overlap. The vegetative activity of the terminal bud ceases when it becomes an inflorescence. Indeterminate types, where flowering and vegetative phases overlap, the terminal bud continues vegetative activity during most of the reproductive flowering period (Zhang and Smith, 1999). With determinate forms, flower, pod and seed development are uniform throughout the plant and consequently seed maturity occurs over a short time range.

Conventional crop production practices require planting crops in well-defined regular spacing and plant density. Two general concepts are often used to explain the relationship between row spacing, plant density, and crop yield (Mellendorf, 2011; Shamsi and Kobraee, 2011). The first concept states that maximum crop yield can only be achieved if the crop community is able to produce sufficient leaf area to provide maximum light interception during reproductive growth. The second one, equidistant

plant spacing maximizes yield because it minimizes interplant competition (Mellendorf, 2011; Shamsi and Kobraee, 2011; Wiggans, 1939). Plant density affects solar radiation interception capacity by the canopy.

The capacity of the crop to capture radiation throughout the crop cycle is closely associated with biomass production at harvest, and therefore, the magnitude of yield (Rondanini et al., 2017; Mataa et al., 2018). Additionally, light quality serves as a sensory cue for the adjustment of plant growth and development (Park and Runkle, 2017). Supra optimal planting density imposes competition for light on plants. Plants perceive the low R/FR ratios principally through the phytochrome B photoreceptor, which promotes the shade avoidance syndrome (SAS), a set of physiological responses that increase the elongation of vegetative structures such as stems and petioles, accelerates flowering, and reduces the number and size of seeds (Smith and Whitelam, 1997). When plant density increases, the reduction of photosynthetically active radiation (PAR) and blue photons partially induce overlapping SAS signaling pathways (Keller et al., 2011).

Due to the increasing importance of soybean in Zambia, new varieties are being developed (SCCI, 2013) and released but production recommendations have not changed to take advantage of emerging varieties variable phenotypic characteristics. The high cost of soybean seed necessitates the re-evaluation and optimization of planting densities recommendations. Soybean yield is considered a function of four basic factors, commonly called 'yield components', which include seed mass, number of seeds/pod, number of pods/plant, and number of plants per given area (Zhang and Smith, 1999).

Phenotypic plasticity has been observed in soybean crop communities in response to seeding rate and row spacing (Mellendorf, 2011). The mechanisms responsible for this yield compensation are not a fully understood subject. Additionally, the degree to which genotypes with different crop growth types exhibit phenotypic plasticity is unknown.

In an earlier study, we investigated the plasticity responses of a number of soybean varieties when subjected to different population density stresses (Sichilima et al., 2018). The findings showed planting density significantly influenced biomass allocation and grain yield. The objective of the current study was to determine if the stress duration or developmental stage at which planting density stress is imposed affects phenotypic plasticity responses and whether plants subjected to such stress can recover after stress removal. Additionally, the study tested the influence of genotype and crop growth type (determinate and indeterminate) on these plasticity responses. Plants subjected to supra-population density at planting were thinned to normal population density at different phenotypic stages so as to achieve variable stress durations. It is anticipated that findings from the study can

help in optimizing crop production and optimal use of seed (and plant population) especially of new varieties.

MATERIALS AND METHODS

Study site

The study was conducted at the Seed Control and Certification Institute situated at 15° 32.772' S and 28° 15.796' E and elevation of 1246 m above sea level in Chilanga district of Lusaka Province of Zambia from December 2015 to April, 2016. Planting was done on the 21st of December, 2015 (which was within the recommended period in Zambia). The soils were a sandy-loam belonging to the Makeni series and classified as *Ultic Haplustalf*. Standard agronomical practices for growing soybean were used to raise the crop (Miti, 1995). At planting, a basal dressing fertilizer was applied at the rate of 20 kg N, 40 kg P₂O₅ and 20 kg K₂O (D Compound) per ha (Miti, 1995). Harvest was done shortly after physiological maturity on 22nd April, 2016.

Plant material

Three varieties were used; Dina, Magoye and Sc Safari (SCCI, 2013). Dina was obtained from MRI/Syngenta Seed Company, it is an indeterminate variety which is non-promiscuous. Magoye was obtained from Zamseed Company and is a promiscuous and determinate variety. Sc Safari is a determinate non-promiscuous variety from SeedCo (Z) Seed Company. The test varieties were chosen because of their high popularity and also due to having contrasting growth characteristics. According to the classification of the International Center of Tropical Agriculture (CIAT 1985), commonly used on dry beans, the growth habits can be classified as: (i) Type I: shrub determinate growth habit, the plants cease the vegetative growth after the insertion of the first floral bud; (ii) Type II: shrub indeterminate growth habit, plants continue their vegetative growth after flowering. They emit few branches and their branches do not emit guides and (iii) Type III: prostrate indeterminate growth habit, with well-developed branch ending in guides. The varieties used in this study were Type I (Magoye and Safari) and II (Dina).

Experimental design and field layout

The trial was laid as a randomized complete block design arranged in a factorial design with two treatments (variety and thinning) replicated four times (Sokal and Rolfe, 1981). The varieties were planted at a planting density of 500,000 plants per hectare and thinned to 400,000 plants which is the recommended spacing in Zambia (Miti, 1995). Thinning was done at four developmental stages that represented key developmental transition stages: V1 (Full expansion of first trifoliolate leaves- transition to autotrophic stage), V3 (Four nodes with 3 unfolded trifoliate), V6 (Seven nodes, with 6 unfolded- unifoliolate, cotyledons senesced maximum branching stage) and R2 (Full bloom with an open flower at the top two nodes of the main stem) (Mc Williams, 1999; Zhang and Smith, 1999). An unthinned treatment was used as control, giving a total of 5 planting densities.

Measured parameters

Plant height

Plant height was measured with use of a ruler at different growth stages, with the final one being at R6-R7 growth stage. At this

point, the plant will have attained its full height and growth would have ceased (Casteel, 2011; Mc Williams, 1999).

Number of branches

The number of branches has a bearing on final yield obtained as pods tend to be borne on the branches. The total number of branches per plant was determined from the average of five randomly selected plants per treatment.

Chlorophyll content

Leaf chlorophyll content was determined by use of chlorophyll meter (Konica Minolta SPAD 502 Plus). The SPAD meter measures green color intensity in leaves *in vivo* and is for collecting large amounts of data on chlorophyll in the field within a short time non-destructively (Moe, 2012).

Biomass

Biomass was obtained by sampling 5 randomly selected plants per replication. The plants were carefully dug up and weighed to get fresh weight then dried at 65°C for 48 h then weighing them again to get dry weight.

Yield

After physiological maturity the pods were harvested and shelled, and seed dried under shade to a 15% moisture content. Yield was calculated as a function of base population, pod number, seeds per pod and seed weight (Casteel, 2011) at the harvestable moisture content of 15%.

Seed weight

Seed weights were obtained by counting 100 seeds in three replicates per treatment, weighing them to come up with a representative 100-seed weight.

Days to 50% flowering

The number of days was calculated from the time of plant emergence to when the plants reached 50% flowering and data was collected at the R1-R2 growth stage. The days to 50% flowering occurs at the time a plant has entered the reproductive phase (UPOV, 1998).

Days to pod filling

In soybean, full seed stage occurs at R6 growth stage and this stage is also known as the "green bean stage" marking maximum pod filling (Mc Williams et al., 1999). It was determined as the total number of days from emergence to this stage.

Days to full maturity

The number of days was thus calculated from emergence to R8. It is the stage when most of the leaves have lost their greenness and marks the plant's whole growth period.

Number of pods per plant

The number of pods per plant was determined by counting pods from a sample of five randomly sampled plants and expressed as the mean number of pods per plant. This was done at the R7-R8 growth stage when all the pods had fully formed and matured. The number of pods per plant is a significant factor in determining the plant yield (Casteel, 2011).

Number of seeds per plant

The number of seed per plant was calculated by multiplying average of locules per pod and pods per plant. Like the number of pods per plant, the number of seeds per plant contributes to the determination of the final yield (Casteel, 2011).

Data analysis

Data was analyzed using GenStat statistical package Version 12 (VSN, 2009). The data was subjected to analysis of variance and where significant treatment effects were detected, mean separation was done using the least significant difference (LSD).

RESULTS

Table 1 summarizes effect of treatments on vegetative and reproductive parameters. Genotype had highly significant effect on most of the parameters measured; days to flowering (length of vegetative phase), biomass, branching, leaf chlorophyll content, plant height, seed weight, and total grain yield. Time of thinning exerted effect on number of branches, plant height, above ground biomass and yield.

Effect on vegetative parameters**Plant height**

The time of thinning was done had a significant effect on plant height (Table 2 and Figure 1). Dina had significantly taller plants compared to Magoye and Sc Safari ($p \leq 0.01$). Unthinned plants or those thinned late (T3 and T4) were significantly taller than thinned early (T1 or T2). The increase in plant height was between 31 and 39% relative to the unthinned treatment. This difference was more evident in the early growth stage (V4).

Biomass

Effects of treatments on biomass are shown in Table 1 and Figure 1. Increasing plant density increased biomass. The early thinned treatments exhibited the highest increase in biomass, the increase was significant in the late vegetative stage (V8) where the unthinned treatments had 13.3 g dry matter per plant, 18 g for the T1 thinning, representing a 35% increase. The increase in biomass decreased with delayed thinning (Figure 1).

Branching

There were no differences in the number of branches among the genotypes (Table 2 and Figure 1). The number of branches increased with thinning, the difference was significant between the non-thinned treatment and those treatments thinned at V3 stage ($p \leq 0.05$). There were no significant differences in number of branches among the other thinning treatments.

Chlorophyll content

The chlorophyll content was not affected by thinning stage but there were differences among genotypes (Table 1 and Figure 2). Chlorophyll content was higher in the variety Sc Safari compared to the other two genotypes ($p \leq 0.05$). There were differences in chlorophyll content among genotypes, however, these differences did not translate in increased productivity or yield as the genotype that had higher chlorophyll (Sc Safari) had low yield relative to the other two.

Effects on reproductive parameters

The effects of treatments on reproductive parameters are shown in Table 2 and Figure 2. Generally, thinning had less effect on reproductive parameters.

Days to 50% flowering

There were differences among the genotypes in the duration of the period to flowering. Sc Safari at 51.7 had the shortest days to flowering and Dina the longest at 66.4 days. Time of thinning did not affect days to flowering. The number of days to flowering is important because it determines the period available for the plant to synthesize and accumulate photo assimilates and these are used for plant development and ultimately yield. The genotype that had the longest days to flowering duration also had the highest yield.

Locules per pod

Genotype had a significant effect on locules per pod. Dina had significantly more locules per pod compared to Sc Safari. Magoye was intermediate. Time of thinning did not affect number of locules per plant.

Number of pods per plant and seeds per plant

The number of pods per plant varied between 20.5 and 34.3, Magoye had significantly more pods per plant and seeds per plant. There was a trend of number of pods per

Table 1. Summary of analysis of variance of planting density and genotype effects on vegetative and reproductive parameters of soybeans.

Parameter ^z	100 SDWT	50%DF	BWT1	BR	CLV4	CLV6	DPF	LPP	NSP	PPD	PHV4	PHR8	RDW	BWT2	YLD
Variety (V)	***	***	***	ns	**	***	***	**	***	***	***	***	ns	***	**
Thinning (T)	ns ^y	ns	ns	**	ns	ns	ns	ns	ns	ns	**	ns	ns	**	**
V × T	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns	ns
CV%	3.9	0.2	5.8	9.3	4.4	1.8	0.1	3.1	6.2	3.9	5.6	6.6	4.7	4.0	8.8

^z100 seed weight (100SDWT); Days to 50% flowering (50%DF); Biomass dry weight/plant at R3 (BWT1); No. of branches/plant (BR); Chlorophyll content at V4 (CLV4); Chlorophyll content at V6 (CLV6); Days to pod filling (DPF); No. of locules/pod (LPP); No. of seeds/plant (NSP); No. of pods/plant (PPD); Plant height at V4 (PHV4); Plant height at R8 (PHR8); Root dry weight (RDW); Biomass weight per plant at R8 (BWT2); Grain yield/hectare (YLD). ^yLevel of significance; ns, **, *** denoting non-significant, significant at $p \leq 0.05$ and $p \leq 0.001$.

Table 2. Effect of planting density on vegetative parameters in selected soybean genotypes

Source of variation	Chlorophyll content ^z	Plant height		Branches per plant	Biomass ^y	Days to Flowering	
		V4	R8				
Variety (V)	Dina	35.6 ^{aw}	22.5 ^b	85.0 ^b	2.89 ^a	18.7 ^b	66.4 ^b
	Magoye	33.5 ^a	18.5 ^a	81.2 ^b	3.35 ^a	15.1 ^a	64.7 ^b
	SC Safari	38.8 ^b	19.7 ^a	57.5 ^a	3.07 ^a	13.8 ^a	51.7 ^a
Thinning time ^y	T0	35.7 ^a	20.0 ^{ab}	73.0 ^a	2.51 ^a	13.3 ^a	61.0 ^a
	V1	36.2 ^a	19.9 ^{ab}	76.8 ^a	3.31 ^{ab}	18.0 ^b	60.6 ^a
	V3	36.4 ^a	19.0 ^a	74.1 ^a	3.49 ^b	17.7 ^b	61.1 ^a
	V6	35.3 ^a	21.2 ^b	73.2 ^a	3.36 ^{ab}	15.1 ^{ab}	61.1 ^a
	R2	36.2 ^a	21.1 ^{ab}	75.7 ^a	2.84 ^{ab}	15.3 ^{ab}	60.9 ^a
Factor significance ^y							
Variety	-	***	***	***	ns	***	***
Planting density	-	ns	**	ns	**	**	ns

^zLeaf chlorophyll content given as SPAD meter reading; ^yTotal biomass measured at V3; ^xThinning time T0 non thinned-maintained at 500, 000 plants per hectare; V1, V3, V6 and R2, respectively thinned from 500,000 to 400,000 plant population at V1, V3, V6 and R2 developmental stages. ^wFigures followed by same letter denote no significant difference. ^vLevel of significance ns, **, *** denoting non-significant, significant at $p \leq 0.05$ and at $p \leq 0.001$.

plant and seeds per plant increasing with thinning, but this trend was not statistically significant (Figure 2) and was more evident in Magoye. Days

to pod filling and days to full maturity were also not affected significantly by genotype or thinning time.

Yield

Planting density had significant effects on yield

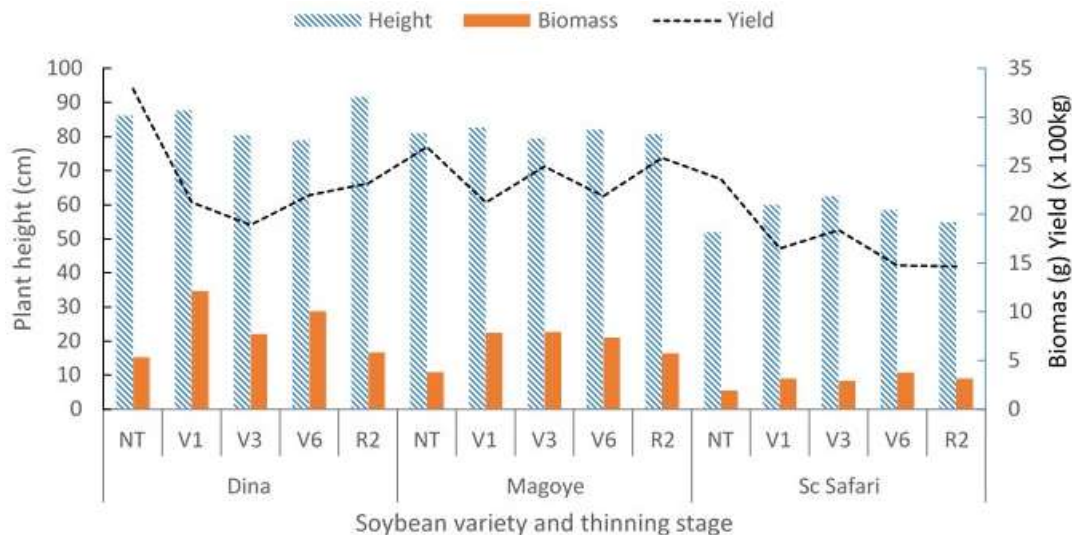


Figure 1. Changes in vegetative parameters (plant height and total biomass) and grain yield in soybeans varieties thinned at various growth stages. NT, non-thinned-(maintained at 500,000 plants/ha); V1, V3, V6, and R2 being soybean developmental stages at which the plants were thinned from 500,000 to 400,000 plant population.

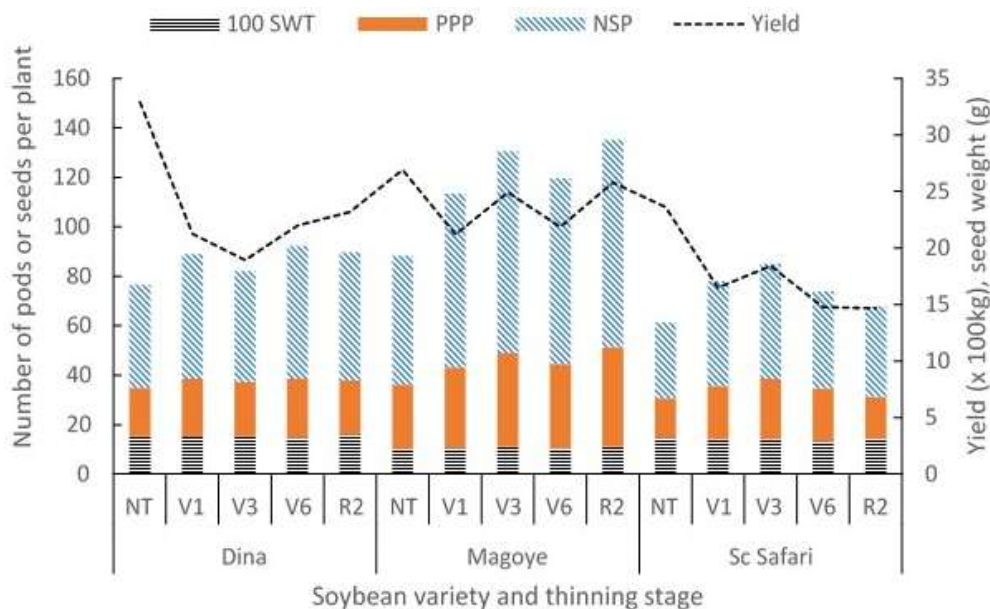


Figure 2. Changes in reproductive parameters (100-seed weight, pods per plant (PPP), number of seeds per plant (NSP) and grain yield in 3 soybeans varieties thinned at various growth stages. NT, non-thinned-(maintained at 500,000 plants per hectare); V1, V3, V6, and R2 being soy bean developmental stages at which the plants were thinned from 500,000 to 400,000 plant population.

shown in Table 3 and Figure 2. Yield was the highest in unthinned treatments and tended to decline with thinning. The late thinning (at V6 and R2) yields were similar to the unthinned treatment (NT). The decline in yield was the most significant with earlier thinning compared to late

thinning with an average reduction in yield of 0.8 ton/ha between the unthinned treatments and the thinned ones. In terms of genotype, Magoye, a determinate variety had significantly higher yield compared to the other 2 varieties across all treatments, although Dina had the highest yield

Table 3. Effect of planting density on reproductive parameters in selected soybean genotypes.

Source of variation		Days to 50 % Flowering	Locules/Pod	Pods/Plant	Seeds/Plant	Seed weight	Grain yield
Variety (V)	Dina	66.4 ^{c z}	2.2 ^b	22.3 ^a	48.4 ^a	15.2 ^c	2.37 ^b
	Magoye	64.7 ^b	2.1 ^{ab}	34.3 ^b	72.6 ^b	10.6 ^a	2.42 ^b
	SC Safari	51.7 ^a	1.9 ^a	20.5 ^a	39.1 ^a	14.0 ^b	1.76 ^a
Thinning time ^y	T0	61.0 ^{ax}	2.0 ^a	20.7 ^a	41.3 ^a	13.3 ^a	2.8 ^b
	V1	60.6 ^a	2.1 ^a	25.9 ^a	54.3 ^a	13.2 ^a	2.0 ^a
	V3	61.1 ^a	2.0 ^a	28.3 ^a	57.6 ^a	13.4 ^a	2.1 ^{ab}
	V6	61.1 ^a	2.1 ^a	26.5 ^a	55.9 ^a	12.8 ^a	1.9 ^a
	R2	60.9 ^a	2.2 ^a	26.5 ^a	57.5 ^a	13.7 ^a	2.1 ^{ab}
Factor significance ^v							
Variety		***	***	***	***	***	***
Planting density		<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	<i>ns</i>	**

^zFigures followed by same letter denote no significant difference. ^yLevel of significance *ns*, ^xThinning time T0 non thinned-maintained at 500, 000 plants per hectare; V1, V3, V6 and R2, respectively thinned from 500,000 to 400,000 plant population at V1, V3, V6 and R2 developmental stages. ^vFigures followed by same letter denote no significant difference. **, *** denoting non- significant, significant at $p \leq 0.05$ and at $p \leq 0.001$.

in the unthinned treatments.

DISCUSSION

Effects of treatments on vegetative development

The results obtained showed significant treatment effects on vegetative parameters especially thinning time on plant height and branching and biomass accumulation. An ecologically important yet environmentally labile aspect of plant development is the ability to vary the proportion of biomass allocated tissues such as roots, leaves, stems and reproductive structures (Bazzaz, 1996). This allows plants to adaptively enhance access to a specific resource in short supply. This altered partitioning is described as allocational

plasticity (Sultan, 2003). Plasticity for biomass allocation to plant tissues is a major means of plant adjustment to the environment. It has been suggested that developmental shifts due to changes in sink; source relationships are mediated through changes in plant growth regulators whose resource costs are minute (Sultan, 1992; Bradford and Hsiao, 1982). Although thinning stage affected biomass allocation, this biomass, however, was directed towards vegetative tissues and not grain yield.

Effects on leaf chlorophyll content

Chlorophyll is an important pigment for light capture and therefore the amount of chlorophyll is critical in increasing the photosynthetic rate and ultimately accumulation of photoassimilates. High

plant densities induce shade effects that can affect leaf chlorophyll content (Mataa and Tominaga, 1998) but this effect was not observed in this study. One possible explanation could be that since soybeans are a leguminous plant that fixes nitrogen-a key component of chlorophyll-and also because the plant density stress developed gradually, the plants were able to adjust and correct any chlorophyll imbalance. As noted earlier by Park and Runkle (2017), De Luca and Hungria (2014), and Ballaré et al. (1990), within a crop community, plants growing under a canopy not only experience a reduction in the amount of irradiance, but also a reduction in the quality of light as chlorophyll preferentially absorbs red light (R) and reflects far-red (FR) light. Many plant species show a range of tolerance to variations in light intensity and this is achieved through morphological, physiological and

allocation plasticity (Sultan, 1992). Photosynthetic plasticity appears to incur little physiological or structural cost (Gross, 1984). Typically, leaves that develop in low-light show changes in chloroplast structure that enhance light harvesting capacity and this is not metabolically costly (Mooney and Gulman, 1979). The results showed that differences in chlorophyll content genotypic were due to genotype but not plant density. It can be postulated that because effects of crop density did not elicit sufficient environment effects to cause significant changes in chlorophyll content, the effects on leaf photosynthesis were minimal.

Effects on reproductive development

The number of locules and seed weight are important determinants of grain yield and it was observed that Dina with slightly more and larger heavier seeds and more locules, also exhibited significantly higher yield. Thinning increased branching and canopy biomass but that biomass was directed towards vegetative tissues and not seed. Thinning (and resultant decreased plant density) did not have significant effects on many yield components possibly because flower induction phase occurs much earlier in the development cycle and by the time thinning was done the process had already terminated (Zhang and Smith, 1999). The yield decline noted in the very early thinned treatment could indicate that the recommended plant population of 400, 000 plants per hectare is lower than optimum and these test varieties can withstand a higher plant density and cause significant yield increase.

Influence of growth characteristics

Changing crop population density modifies resource availability to individual plants. The ability to use these resources depends on plant strategies that induce vegetative and reproductive plasticity (Rondanini et al., 2017; Roiloa et al., 2014). Plasticity responses to the environment are dynamic and vary with time (Murren et al., 2015). It has been postulated that modular organisms (plants with indeterminate growth characteristics) may compensate for any negative impacts through flexible addition of new modules (Murren et al., 2015). In general, plants with indeterminate growth habit have higher total cycle and height of plants in relation to the determinate growth habit (Velho et al., 2018). Although, the present study included varieties that had contrasting growth characteristics (determinate and indeterminate), no differences were observed between the two different growth categories except for yield. It was interesting to note that whereas in this study we varied the duration and/or timing of population density stress, similar results were obtained in a related study where we had a

constant population stress duration (Sichilima et al., 2018).

Conclusion

The soybean varieties used in this study exhibited significant vegetative plasticity. Reducing plant density especially in early vegetative phases reduced plant height, increased branching and biomass allocation to vegetative plant parts. However, these effects did not always increase yield. The growth type of the variety tested, whether determinate or indeterminate, did not appear to exert any significant influence on plasticity.

CONFLICT OF INTERESTS

The author has not declared any conflict of interests.

REFERENCES

- Ballaré CL, Scopel AL, Sánchez RA (1990). Far- red radiation reflected from adjacent leaves: an early signal of competition in plant canopies. *Science* 247:329-332.
- Bazzaz FA (1996). *Plants in changing environments: Linking physiological population and population ecology*. Cambridge University Press, Cambridge.
- Bradshaw AD (1965). Evolutionary significance of phenotypic plasticity in plants. *Advances in Genetics* 13:115-155.
- De Luca MJ, Hungria M (2014). Plant densities and modulation of symbiotic nitrogen fixation in soybean. *Scientia Agricola* 71:181-187.
- Grime JP (1977). Evidence for the existence of three primary strategies in plants and its relevance to ecological and evolutionary theory. *American Naturalist* 111:169-1194.
- Grime JP, Mackey JML (2002). The role of plasticity in resource capture by plants. *Evolutionary Ecology* 16:299-307.
- Grime JP, Crick JC, Rincon JE (1986). The ecological significance of plasticity. In: *Plasticity in Plants*. Jennings DH and Trewavas AJ. (eds). Company of Biologists, Cambridge University Press, Cambridge.
- Keller MM, Jaillais Y, Pedmale UV, Moreno JE, Chory J, Ballaré CL (2011). Cryptochrome 1 and phytochrome B control shade-avoidance responses in Arabidopsis via partially independent hormonal cascades. *Plant Journal* 67:195-207.
- Larsen DW, Kershaw KA (1975) Acclimation in arctic lichens. *Nature* 254:421-423.
- Mataa M, Tominaga S (1998). The Effects of shading stage and level on fruit set and development, leaf carbohydrates and photosynthesis in ponkan (*Citrus reticulata* Blanco). *Japanese Journal of Tropical Agriculture* 42:103-110.
- Mataa M, Makungu B, Siziya I (2018). Shading effects of intercropping roselle (*Hibiscus sabdariffa*) genotypes on plant development, assimilate partitioning and leaf nutrient content. *International Journal of Agricultural Research Innovation and Technology* 8:7-13.
- Mellendorf EN (2011). Soybean growth and yield response to interplant competition relief in various plant density environments. MSc. Thesis (unpublished), University of Illinois at Urbana-Champaign pp. 11-12. www.ideals.illinois.edu/bitstream/handle/2142/26104/Mellendorf_Nat_han.pdf
- Miti JM (1995). Soybean (*Glycine max* (L) Merr.). In: *Zambia Seed Technology*, Muliokele SW. (ed), Lusaka: Ministry of Agriculture, Food and Fisheries pp. 195-199.
- Moe S (2012). Relationships of Soybean (*Glycine max* L.) accessions based on Agro-Morphological, Physiological Traits and DNA

- Polymorphisms. MSc. Thesis (unpublished), Suranaree University of Technology.
- Mooney HA, Gulman SL (1979). Environmental and evolutionary constraints on photosynthetic characteristics of higher plants, in: Topics in plant population biology Solberg O. Jain S. (eds). New York. Columbia University Press pp. 316-337.
- Murren CJ, Auld JR, Callahan H, Ghalambor CK, Handelsman CA, Heskell MA, Kingsolver JG, Maclean HJ, Masel J, Maughan H, Pfennig DW (2015). Constraints on the evolution of phenotype plasticity: limits and costs of phenotypes and plasticity. *Heredity* 115:291-301.
- Nicoglou A (2015). The evolution of phenotypic plasticity: Genealogy of a debate in genetics. *Studies in History and Philosophy of Science Part C: Studies in History and Philosophy of Biological and Biomedical Sciences*, Elsevier 50:67-76. <10.1016/j.shpsc.2015.01.003>. <halshs-01498558>
- Park Y, Runkle ES (2017). Far-red radiation promotes growth of seedlings by increasing leaf expansion and whole-plant net assimilation. *Environmental and Experimental Botany* 136:41-49.
- Rolao SR, Rodriguez-Echeverria S, Lopez-Otero A, Retuerto R, Freiteras H (2014). Adaptive plasticity to heterogeneous environments increases capacity for division of labor in the clonal invader *Caprobotus edulis* (Aizoacea). *American Journal of Botany* 101:1301-1308.
- Rondanini DR, Menendez YC, Gomez NV, Miralles DJ, Botto JF (2017). Vegetative plasticity and floral branching compensate low plant density in modern spring rapeseed. *Field Crop Research* 210:104-113.
- Seed Control and Certification Institute (SCCI) (2013). Variety Register: Seed Control and Certification Institute, Chilanga, Zambia. http://www.agriculture.gov.zm/?page_id=4819
- Schmalhausen I (1986). *Factors of evolution* (reprint of 1949 edition). University of Chicago Press.
- Sekimura T, Roose T, Maini PK, Suzuki J, Hara T (2000). The Effect of Population Density on Shoot Morphology of Herbs in Relation to Light Captured by Leaves. *Ecological modeling*. Elsevier Science B. V.
- Shamsi K, Kobraee S (2011). Soybean Agronomic responses to plant density. *Scholars Research Library. Annals of Biological Research* 2:168-173.
- Sichilima I, Mataa M, Mweetwa AM (2018). Morpho-physiological and yield responses associated with plant density variation in soybean [*Glycine max* L. (Merrill)]. *International Journal of Environment, Agriculture and Biotechnology* 3:274-285.
- Smith H, Whitelam GC (1997). The shade avoidance syndrome: multiple responses mediated by multiple phytochromes. *Plant Cell Environment* 20:840-844.
- Sokal RR, Rolfe FJ (1981). *Biometry*, Second edition. W. H. Freeman and Company, New York pp. 394-399.
- Sultan S (1992). Phenotypic plasticity and the Neo-Darwinian legacy. *Evolutionary Trends in Plants* 6:61-71.
- Sultan S (2003). Phenotypic plasticity: a case study in ecological development. *Evolution and Development* 5:25-33.
- Velho LP, MELO RC, Bernardy JP, Grigolo S, Guidolin AF, Coimbra JL (2018). Root distribution and its association with bean growth habit. *Anais da Academia Brasileira de Ciências* 90(2):1837-1844.
- VSN International (2009). Numerical Algorithms Group. www.nag.co.uk
- Wiggans RG (1939). The influence of space and arrangement on the production of soybean plants. *Agronomy Journal* 31:314-321.
- Zhang F, Smith DL (1999). Soybean [*Glycine max* (L.) Merr.] physiology and symbiotic dinitrogen fixation. In: *Crop yield: physiology and processes*. Smith, DL. C. Hamel (eds.). Springer, (Berlin) pp. 375-399.