

Full Length Research Paper

Effects of shade and drought stress on soybean hormones and yield of main-stem and branch

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Accepted 19 September, 2011

Multiple frequently interactive stress factors naturally influence plant due to global change. The leaf's hormone concentrations, main-stem and branch yield response to the combination of shade and drought were studied in a greenhouse experiment during 2009 and 2010 seasons. Pot experiments were conducted under shade of maize (LI) and normal irradiance (HI). Shade stress was removed once maize was harvested. Manipulative progressive soil drying period at branching stages under good soil conditions (HW) and water stress treatment (LW) were applied in 2010, while well-watered (WW) and moderate drought (MD) were applied in 2009. Under shade stress, seedling height and first internode length increased, stem diameter decreased, abscisic acid (ABA) and zeatin (ZT) concentration decreased, while indole acetic acid (IAA) and gibberellins 3 (GA3) concentration increased. More also, branch numbers, pod number of branches and seed number of branches increased. Branch yield did not reduce significantly under shade stress, which was related to the decrease of ABA and IAA. Based on the results, soybean yield decreased under shade and drought stresses was mainly due to the yield reduction of the main-stem.

Key words: Abscisic acid, indole acetic acid, relay strip intercropping system, soybean, zeatin.

INTRODUCTION

As a result of population increase, the demand of food is ever increasing (Godfray et al., 2010). It is particularly important to increase the multiple crop index of land for the development of grain production. As the benefits of intercropping facilitation, yield advantage, high utilization efficiency of light and water, pest and disease suppression, biological nitrogen fixation and legume /non-legume intercropping system are widely used in the world (Ghanbari et al., 2010; Li et al., 2009). In China, half of the total grain yield is produced with multiple cropping; wheat/corn/soybean relay strip intercropping system is popular in South China (Yan et al., 2010). Plants are usually exposed to several stresses simultaneously under field conditions, with limit of light and water availability being the main environmental factors affecting relay strip

intercropping soybean. These stresses may cause a variety of plant responses which can be additive, synergistic or antagonistic.

Seed yield of soybean is produced on both the main-stem and the branches originating from main-stem node (Board, 1987; Cho et al., 2005). Majority of the seed yield of determinate soybean is produced on these branches (Board, 1987). Unfavorable growing conditions such as excessive soil water and agricultural practices such as late planting, reduction in the ratio of red to far-red light (R : FR) and high plant density, reduce seed yield primarily by reducing branch growth and branch seed yield per plant (Green-Tracewicz et al., 2010). Water stress at the seedling and at the flowering stage decreases soybean yield by 20 and 46%, respectively (Shou et al., 1991) due to decreased photosynthetic rate, stomatal conductance and transpiration rate of soybean (Ohashi et al., 2006; Vu et al., 2001). Moreover, shade treatments have been shown to reduce yield and seed

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Table 1. Weather data for each month of soybean growth stage during 2009 and 2010 seasons.

Year	Month	Maximum temp. (°C)	Minimum temp. (°C)	Average temp. (°C)	Relative humidity (%)	Precipitation (mm)	Day length per month (h)
2009							
	May	22.2	15.3	20.5	46.7	69.0	172.1
	June	29.4	18.2	23.6	42.9	143.4	178.3
	July	27.5	20.4	25.1	43.2	219.6	202.1
	August	26.2	23.2	24.8	39.2	170.3	207.5
	September	25.4	19.5	23.1	42.3	122.7	169.4
	October	20.1	12.4	17.4	44.3	59.1	141.2
2010							
	May	20.1	14.3	19.3	45.9	50.2	162.2
	June	27.3	17.4	20.9	43.1	98.4	160.4
	July	26.2	19.4	24.4	42.4	131.9	192.1
	August	22.5	24.3	23.7	38.5	236.7	197.5
	September	24.6	16.2	20.9	41.5	213.1	161.3
	October	17.7	11.1	15.4	43.5	139.6	135.2

Data from the Sichuan Province Meteorological Institute.

size (Tang et al., 2010) and also to reduce yield with no effect on seed size (Andrade and Ferreiro, 1996).

Hormones are critical to maintain branches; shoot branching is highly regulated by endogenous and environmental cues (Umehara et al., 2008). Auxin and cytokinin have long been known to have an important involvement in controlling shoot branching (Leyser, 2003) since auxin suppresses axillary bud outgrowth and cytokinin promotes axillary bud outgrowth (Shimizu-Sato et al., 2009). Hormones always have advantages to maintain yield and ameliorate the opium yield (Khan et al., 2007). Drought and shade stress have effects on auxin, cytokinins and abscisic acid concentrations (Davies, 2010). This study investigates the impact of temporary shade combined with water stress on the response of hormones and branches yield. Our aims were to (1) determine hormones concentration and branch yield as affected by drought, shade stresses and their combination and (2) elucidate the relation between hormones and branch yield.

MATERIALS AND METHODS

Plant material and growth conditions

Soybean cultivar Gongxuan No.1 (GX), a major component of South-western soybean cultivars, was tested in the experiments of 2009 and 2010. Each seed was weighed individually and sown (in May 2009/2010) in cylindrical pots of 14-L volume (23 cm high × 28 cm diameter), which contained 13 kg soil with 50% sand, 47.5 clay and 2.5 organic matter. The mixed soil with fertilizer consisted of N = 0.355 g, P₂O₅ = 0.556 g and K₂O = 0.406 g. Fertilizers were applied

after emergence, with 3 g single super phosphate, 1 g potassium sulfate and 1.5 g urea per pot. The experiment was carried out in a shed of Sichuan Agricultural University (29059' N, 103000' E; at an altitude of 500 m; the weather data in 2009 and 2010 are listed in Table 1) with an automatic closure system of upper ceiling when it was rainy.

The soybean seeds were harvested in late October 2009 and 2010, respectively. Soybean were subjected to two light levels:(1) high irradiance treatment (HI), which received normal radiation from sun when it was sunny and received available radiation inside the shed when it was rainy (2009, 2010); (2) low-irradiance treatment (LI), which was covered by a light screen (Yaan Nongzhi CO., China, 2009) and under the shade of corn (2010). In the experiment of 2010, the light penetration through the corn canopy to the soybean was 80% when the soybean was sown, 65% at the vegetative stage V5, 72% at the reproductive stage R1 and 70% when the soybean plant in reproductive stage R2 corn was at maturity. In 2009, the light penetration through the light screen to the soybean was 65%. Each of the watering treatments was set up within each shade frame and replicated four times, each by one plant in a single pot.

Pots were watered every two days during the first period of the experiment. Once the soybean seedlings reached V5 stage (at the end of July 2009/2010) and two months after sowing (at the end of May 2009/2010), half of the pots stopped receiving any watering (low-water treatment, LW) while the other half was kept continuously moist (high water treatment (HW); 75 ± 2% of the soil field capacity) in 2010. In 2009, half of the pots were kept continuously moist (WW; 75 ± 2% of the soil field capacity) and at moderate drought (MD; 45 ± 2% of the soil field capacity). In 2010, low-water treatment simulated a typical climate situation of seasonal drought in south-western China, compared with a continuously moist one (HW). The experimental light treatments simulated the field conditions in the relay strip intercropping system, distinguishing two types of microhabitat: sloe cropping soybean (HI) and under corn cover (LI). During the experiment in 2010, we measured soil moisture (in volumetric water content, VWC), measured along the first 20 cm depth (with a TRIME-PICO, German) daily in a subsample of five

Table 2. Soil water content percentage (WC %) at the beginning, middle and end of the experiment (mean \pm SE) in a subsample of pots under the two light and two water levels combinations during 2010 season.

Time (d)	Low water		High water	
	HI	LI	HI	LI
0	80 \pm 0.8	80 \pm 1.2	79 \pm 1.4	80 \pm 0.8
10	51.8 \pm 0.7	53.7 \pm 1.1	76 \pm 0.9	78 \pm 1.1
20	25.5 \pm 0.6	29.8 \pm 0.2	79 \pm 0.8	81 \pm 1.1

HI represents high irradiance (normal light) and LI represents low irradiance (under the shade of maize).

pots under different light and water treatments. Pots under LW decrease their water content differently for the two light treatments (Table 2).

Morphological measurement

Seedling height, stem diameter, the first internode length and branch numbers per plant were determined at growth stage R5 (initial seed fill), about 14 days after re-watering; effective branch numbers were determined at maturity; each treatment had four replications.

Plant hormones

Instruments and reagents

Varian Pro STAR 240 high performance liquid chromatograph and a Milli-Q ultrapure water purification system were used (Tang et al., 2010). Standards of abscisic acid (ABA), indole acetic acid (IAA), gibberellins 3 (GA3) and zeatin (ZT) were from Sigma Chemical, chromatographic purity methanol was from Fisher Chemical, ethanoic acid was of analytical grade and the water used in the experiment was ultrapure water.

Chromatography

A Hypersil ODS C18 chromatographic column (150 \times 4.6 mm, 5 μ M) was used (Tang et al., 2010), employing as mobile phase a mixture of methanol and 0.6% ethanoic acid. Gradient elution was applied as follows: 5 to 75% methanol from 0 to 13 min, and 75% methanol from 13 to 15 min. Column temperature was 30°C, sample size was 10 μ l, flow rate was 1 ml.min⁻¹ and UV detection wavelength was 254 nm.

Determination of hormone levels

Determinations of IAA, ABA, GA3 and ZT were performed on the same sample; samples were harvested 14 days after drought stress in 2009 and nine days after no water in 2010 (when the leaf water content significantly decreased). The method of Tang et al. (2010) was used.

Yield measurement

Branches were separated from the main stem so the yield and yield components on the branch and main-stem fractions could be determined separately; each treatment had four replications.

Statistical analysis

The experiments were laid out as a split plot design based on randomized complete block design (RCBD). Each treatment was replicated four times. Results were analyzed by two-way analysis of variance and means were compared by LSD test at $P < 0.05$ and $P < 0.01$, using the software Statistical Package for the Social Sciences (SPSS) version 11.5.

RESULTS

Seedling growth

The seedling height, stem diameter and first internode length decreased under drought stress, seedling height and first internode length were increased by shade treatment, while stem diameter decreased by shade treatment. Drought treatment also decreased branch numbers, while shade treatment increased branch numbers (Table 3). Under HI, WW in 2009 and HW in 2010 had the biggest stem diameter; WW and HW under low irradiance (LI) had the most branch numbers, the highest plant height and the longest first internode length.

Plant hormones

The concentration of growth promoting hormones, IAA, GA3 and ZT decreased under drought stress, whereas, that of stress hormone ABA increased with decrease in moisture content of soil. Under shade stress, ABA and ZT decreased, but IAA and GA3 content increased (Table 4). ABA concentration under HI of MD and LW was the highest, while ZT concentration under HI of WW and HW was the highest. WW and HW under LI had the lowest ABA content, the highest IAA and GA3 concentration.

Branch numbers and yield

Drought and shade stress decreased main-stem pod number per plant, main-stem seed number per plant, 100-seed weight, and effective branch numbers per plant, but increased branch pod number per plant, and branch

Table 3. Effects of drought and shade on plant growth of soybean.

Parameter		Plant height (cm)	Stem diameter (cm)	The first internode length (cm)	Branch numbers
2009					
HI	WW	53.76 ^{cc}	0.5205 ^{aa}	3.52 ^{cb}	3.9 ^{aa}
	MD	46.83 ^{dd}	0.4925 ^{bb}	3.33 ^{cb}	1.3 ^{cc}
LI	WW	75.94 ^{aa}	0.4556 ^{bcBC}	10.12 ^{aa}	4.0 ^{aa}
	MD	63.60 ^{bb}	0.4258 ^{cc}	7.55 ^{ba}	2.4 ^{bb}
2010					
HI	HW	51.66 ^{cc}	0.5487 ^{aa}	4.60 ^{bcB}	4.2 ^{aa}
	LW	44.85 ^{dd}	0.5368 ^{baB}	4.38 ^{cb}	1.3 ^{bb}
LI	HW	79.33 ^{aa}	0.4554 ^{bcAB}	8.58 ^{aa}	4.6 ^{aa}
	LW	64.96 ^{bb}	0.4343 ^{cb}	6.02 ^{baB}	1.7 ^{bb}

HI, normal irradiance; LI represents low irradiance, under the shade of light screen or corn. WW, well water (75±2% of the soil field capacity); MD, moderate drought (45 ± 2% of the soil field capacity); LW, low-water treatment; HW, high water treatment. Within columns means in the same season followed by the same small and capital letters are not significantly at the 0.05 and 0.01 levels of probability according to LSD test, respectively.

Table 4. Effects of drought and shade on plant hormone of soybean.

Parameter		ABA (ng g ⁻¹ FW)	IAA (ng g ⁻¹ FW)	GA ₃ (ng g ⁻¹ FW)	ZT (ng g ⁻¹ FW)
2009					
HI	WW	26.62 ^c	47.36 ^c	227.29 ^{bc}	52.66 ^a
	MD	358.55 ^a	22.15 ^d	205.64 ^c	38.08 ^b
LI	WW	14.55 ^c	117.07 ^a	411.81 ^a	49.01 ^a
	MD	285.79 ^b	78.08 ^b	278.74 ^b	33.46 ^b
2010					
HI	HW	24.50 ^c	79.60 ^b	128.29 ^c	37.45 ^a
	LW	207.41 ^a	61.86 ^b	104.01 ^c	30.86 ^{ab}
LI	HW	15.57 ^c	136.06 ^a	300.26 ^a	32.87 ^a
	LW	125.12 ^b	76.55 ^b	274.58 ^b	24.61 ^b

HI, normal irradiance; LI, low irradiance, under the shade of light screen or corn; WW, represents well water (75 ± 2% of the soil field capacity); MD, moderate drought (45 ± 2% of the soil field capacity); LW, low-water treatment; HW represents high water treatment. Within columns means in the same season followed by the same small letters are not significant at the 0.05 and 0.01 levels of probability according to LSD test, respectively.

seed number per plant (Table 5). Main-stem pod number per plant and main-stem seed number per plant was lowest in the treatment of MD and LW of LI; they were the highest in WW and HW of HI. Branch pod number per plant and branch seed number per plant were highest under the treatment of MD and LW of HI; they were the smallest under the treatment of WW and HW of HI. Yield under WW and HW of HI was the highest, but was the lowest under MD and LW of LI. Effective branch numbers

per plant was highest under WW and HW of LI, and they were the lowest under MD and LW of HI.

Interaction of drought and shade on some structural traits, plant hormone and yield

There were significant interactions on plant height, IAA concentration, main-stem seed numbers, and effective

Table 5. Effects of drought and shade on yield and yield components of soybean.

Parameter		Main-stem pod number (plant ⁻¹)	Branch pod number (plant ⁻¹)	Main-stem seed number (plant ⁻¹)	Branch seed number (plant ⁻¹)	100-seed weight(g)	Yield (g pot ⁻¹)	Effective branch numbers (plant ⁻¹)
2009								
HI	WW	14.2 ^a	7.4 ^b	30.2 ^{aA}	11.1 ^b	24.96 ^a	18.20 ^{aA}	2.8 ^{aA}
	MD	12.6 ^b	10.8 ^a	16.5 ^{cC}	28.7 ^a	19.64 ^{ab}	15.52 ^{cB}	1.9 ^{bB}
LI	WW	12.5 ^b	8.4 ^{ab}	20.8 ^{bB}	13.5 ^{ab}	20.67 ^{ab}	17.25 ^{bA}	3.1 ^{aA}
	MD	12.1 ^b	9.6 ^{ab}	17.8 ^{cC}	17.8 ^{ab}	18.06 ^b	14.59 ^{dB}	2.1 ^{abAB}
2010								
HI	HW	8.0 ^a	7.2 ^b	12.7 ^{aA}	11.3 ^b	25.47 ^{aA}	19.59 ^{aA}	3.1 ^{aA}
	LW	5.9 ^b	13.6 ^a	10.5 ^{abAB}	21.4 ^a	20.55 ^{bB}	14.09 ^{bB}	1.7 ^{bB}
LI	HW	5.0 ^b	7.8 ^{ab}	7.4 ^{bB}	13.4 ^{ab}	19.68 ^{bB}	13.24 ^{bB}	3.5 ^{aA}
	LW	4.6 ^b	9.9 ^{ab}	4.0 ^{cC}	17.8 ^{ab}	16.51 ^{cB}	12.24 ^{bB}	1.9 ^{bB}

HI, normal irradiance; LI, low irradiance, under the shade of light screen or corn. WW, well water (75 ± 2% of the soil field capacity); MD, moderate drought (45 ± 2% of the soil field capacity); LW, low-water treatment; HW, high water treatment. Within columns means in the same season followed by the same small and capital letters are not significantly at the 0.05 and 0.01 levels of probability according to LSD test, respectively.

branch numbers (Table 6). According to the data in the two years, shade and drought stress had significant effects on plant height, stem diameter, concentrations of ABA, IAA, ZT and GA3, main-stem seed numbers, 100-seed weight and yield. The effects of drought on branch numbers, branch pod number, branch seed number and effective branch numbers were significant.

DISCUSSION

Researches revealed that elongated plants were more fit at high density and suppressed plants were more fit at low density (Dudley and Schmitt, 1996), elongated stem according to a significant more growth in first internode maybe beneficial to increase the light capture for soybean in relay strip intercropping system. IAA is a major plant growth regulator affecting plant development and it is the predominant auxin in most plants (Garcia-Martin et al., 2005). Shaded soybean had higher seedling height and higher IAA concentration. Seedling height and IAA concentration had positive correlation; $y = 0.001x_2 + 0.067x + 44.02$, $r = 0.8944 > r_{0.001} = 0.8721$ ($n = 8$), so that IAA concentrations appeared to significantly affect soybean seedling height. It was decreased under drought stress, which was beneficial to inhibit vertical growth and avoid lodging for shade soybean.

ABA is thought to act as a messenger in stress perception response pathways in environmental stresses (Zhu, 2002). A high level of ABA in crop floral structures has been thought to be a factor inducing reproductive

abortion under drought conditions (Liu et al., 2003). ABA tended to have lower content under shade stress compared to normal irradiance; such a result might be beneficial to reduce pod abortion. In Emery's research, results show that decreased ABA was associated with continued strong growth of the main stem apex following a decline in CK: IAA ratio. ABA may therefore be a growth inhibitor (Emery et al., 1998). The decrease of ABA concentration under shade stress and the reduction of IAA concentration under drought stress may be beneficial in maintaining more branch numbers for shaded soybean under drought stress. Meanwhile, the relay strip intercropping soybean had its own independent growth period after corn was harvested. At the independent stage, there were more irradiances resources for use, the change of red: far red ratio maybe beneficial to soybean to form more branches. Drought stress occurring between initial flowering and seed fill decreases total seed yield primarily by reducing branch vegetative growth, which reduces branch seed number and branch seed yield (Frederick et al., 2001).

In our research, the branch pod and seed number did not reduce significantly under drought and shade stresses, but rather they increased under drought stress oppositely. Such results may be related to the growth stage; the stresses happened in V5 stage. Soybean had better morphological and physiological elasticity and decrease of ABA for shaded soybean and reduction of IAA for water deficit soybean. Yield decrease of shade and drought stresses was mainly due to yield reduction of the main-stem. Hence, soybean genotype which has better

Table 6. Results of the two-way ANOVA for some structural and physiological leaf traits, according to the factors light (L) and water (W) treatments.

Trait	2009				2010			
	Factor		Interaction	R ²	Factor		Interaction	R ²
	L	W			L	W		
Structural traits								
Plant height	77.5***	11.2***	2.1*	85.8	75.2***	17.9***	1.0**	94.1
Stem diameter	18.4***	14.8**	0.2	33.4	12.4***	28.5***	1.0	42.0
The first internode length	38.8***	5.7	7	51.5	35.3***	4.4	5.3	45.0
Branch numbers	1.0	50.3**	2.9	54.2	3.4	61.0**	2.2	66.5
Plant hormone								
ABA	34.1***	59.2***	0.9	94.2	30.4***	60.6**	0.4	91.4
IAA	51.9**	35.2*	6.7*	93.8	44.4**	34.3*	8.4*	87.1
GA ₃	24.2**	14.4*	0.2	38.8	26.1**	12.3*	1.2	39.6
ZT	36.1***	7.5*	4.2	47.7	39.6***	9.5*	6.2	55.3
Yield and yield components								
main-stem pod number	11.8	3.1	8.6	23.4	15.9	5.3	2.4	23.5
branch pod number	0.0	23.2*	5.2	28.5	4.2	31.9*	8.4	44.5
main-stem seed number	13.1***	56.5***	22.6***	92.2	50.3***	25.5**	11.1**	86.6
branch seed number	4.5	29.3*	10.7	44.6	0.4	38.0*	5.9	44.2
100-seed weight	15.6	28.4*	3.3	47.5	1.5	31.7***	46.8***	80.0
yield	7.1***	57.5***	0.1	64.6	32.3***	9.7**	20.3**	62.3
Effective branch numbers	0.4	72.8***	17.2***	90.4	9.8	25.5*	3.9	39.2

The proportion of the explained variance (SSx / SS_{total}) and the level of significance (*, P < 0.05; **, P < 0.01; ***, P < 0.001) for each factor and the interactions are indicated. R² is the proportion of total variance absorbed by the model.

main-stem yield stability may be suggested under the environment of low irradiance and soil moisture.

ACKNOWLEDGEMENT

The research was supported by National Program on Key Basic Research Project (2011CB100402), Public Research Funds Projects of Agriculture, Ministry of Agriculture of the P.R. China (201103001), Programme on Industrial Technology System of National Soybean (CARS-04-PS19), and National Natural Science Foundation of China (31071373). The author Jing Zhang is a recipient of a scholarship from the China Scholarship Council.

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