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Quantifying soil moisture deficit effects on soybean yield and yield component distribution patterns

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Abstract

Soil moisture stress is the major abiotic stress factor that causes extensive losses to soybean production worldwide. Quantitative relationships between soil moisture deficit and yield components are needed to improve algorithms of the existing soybean models predictability. The objective of this study was to quantify water stress effects on various plant growth and reproductive traits using two soybean cultivars with distinct growth habits, indeterminate type, Asgrow AG5332 and determinate type, Progeny P5333RY. Plants grown in pots outdoors were moved into sunlit controlled environment at flowering stage. Five water stress treatments, 100, 80, 60, 40, and 20% of daily evapotranspiration of the control, were imposed at flowering and continued until maturity. Plant height and node numbers were recorded at 7-day intervals. Plant component dry weights, pod distribution patterns, and pod and seed yield were measured at the final harvest. A quadratic function best described the relationship between soil moisture content and midday leaf water potential and −1.0 MPa leaf water potential was achieved at optimum soil moisture content of 0.15 $m^3 m^{-3}$ soil. The middle region of the canopy in both cultivars accounted for about 60% of final yield compared to top and bottom regions. Branch pod yield was about threefold as high as mainstem yield, and it was more sensitive to moisture stress than mainstem yield. Harvest index declined linearly with decreasing soil moisture levels in the cultivars, and rate of decline in Asgrow AG5332 was lower (slope = 1.68) than the decline of Progeny P5333RY (slope = 2.42) $m^3 m^{-3}$. The functional relationships between soil moisture stress and yield components will be useful to aid farm managers in scheduling irrigation and to improve the functionality of soybean crop models under varying soil moisture conditions.

Abbreviations

DAP	Days after planting
ET	Evapotranspiration
HI	Harvest index
HSW	100-seed weight
LWR	Leaf water potential
SPAR	Soil–plant–atmosphere–research
SEM	Standard error of the mean
SN	Number of seeds
SY	Seed yield

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Introduction

Soybean, *Glycine max* (L.) Merr., is the world's leading economic oilseed crop which provides essential proteins for both human and animal nutrition. The United States Department of Agriculture estimates that the worldwide soybean production in 2017/2018 will be 351 million metric tons (mt) (USDA 2017). In the year 2016, USA was the country with the greatest soybean output, producing 116 mt, followed by Brazil (107 mt), Argentina (57 mt), and China (14 mt) (USDA 2017). Regardless of the amplified global demand, soybean yield losses due to erratic precipitation and limited ground water reservoirs continue to reduce the crop production sustainability across the world (Le et al. 2012). Hence, it is crucial to develop some strategies for coping with the effects of moisture stress to assist in stabilizing yield under stress conditions (Ries et al. 2012).

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Among many other environmental stresses that affect crop production (Brand et al. 2016; Reddy et al. 2017; Wijewardana et al. 2015, 2016a, b), soil moisture stress is considered as the most damaging abiotic stress limiting soybean yield in the U.S.. Persistent soil moisture stress over many parts of United States has become the major limitation of soybean yield (Dai 2013; Zipper et al. 2016). Currently, only about 53% of soybean hectarage in Mississippi is irrigated (Kebede et al. 2014); therefore, unpredictable rainfall combined with shallow claypan soils with lesser water availability make soil moisture stress a risk. In the US mid-South, the occurrence of extended soil moisture stress during summer turned out to be progressively common in recent years. The depletion in the Mississippi River Alluvial Aquifer system, which is used to irrigate most crops in the Mississippi Delta, implicates the unsustainability of crop production in the region (Kebede et al. 2014). Therefore, it is necessary to place an effort to understand the morphological and reproductive attributes that govern drought tolerance with an aim of increasing soybean yield under soil moisture stress to mitigate the impacts of droughts in the current and in the near-future environments.

Crop simulation models are important to incorporate the interdisciplinary knowledge acquired through research and technological advancements in several scientific fields related to agricultural production systems. There has been a tremendous increase in modeling soybean growth to understand the timing of crop developmental stages and to predict reproductive performance under numerous environmental conditions. Currently, many soybean crop models are available such as GLYCIM, DSSAT CSM–CROPGRO, APSIM (Keating et al. 2003), SOYSIM, MONICA (Nendel et al. 2011), AQUACROP, and FAO—agroecological zone (Battisti and Sentelhas 2015) to predict the crop yield and to identify tolerant traits under wide range of environments. To improve accuracy and reduce uncertainties in the existing crop models when validating data in the field and forecasting yields for management, several comparative studies are still required across different environments. Therefore, quantifying several growth and reproductive aspects of soybean and incorporating those functions into soybean simulation models are imperative to evaluate the causes of yield variability in current and future climates.

Soybean stem extension has shown to be controlled by *Dt1* locus (Tanaka and Shiraiwa 2009) and thus controlling overall canopy development and plant physique. There are two broad types of stem growth habit in soybeans, as indeterminate and determinate based on the timing of the cessation of apical stem growth (Tian et al. 2010; Ting 1946). The indeterminate, which are the most common and early maturing types in northern part of USA, continue to develop new leaves even after the floral induction until photosynthate demand by developing seeds causes a termination in the production of vegetative dry matter (Tian et al. 2010). In contrast, late-maturing determinate types cease vegetative activity at or soon after photoperiod-induced floral induction. Because of that, generally, determinate types have a bushier canopy with a shorter mainstem length. However, the agronomic significance of such differences in stem growth habit on yield traits and yield component distribution under adverse conditions like soil moisture stress have not reported.

Soil moisture stress is like a syndrome that affects all plant processes (Salekdeh et al. 2009). Remarkable efforts have been put on the improvement of soil moisture stress tolerance of soybean, with a primary goal of enhancing yield under moisture deficit. In general, soil moisture is critical for optimum growth during the very early vegetative stage and from flowering through the seed-filling period for soybeans (Brevedan and Egli 2003). At the early vegetative stages, soil moisture stress can impact yield by reducing the number of mainstem nodes and branches that develop, whereas, at later stages, water deficit can accelerate leaf senescence and shorten the period of seed-filling (Brevedan and Egli 2003). Soybean pod set and seed development are more vulnerable to soil moisture stress leading to a substantial yield reduction. Brown et al. (1985) reported a significant yield loss when soil moisture stress was at initiated R2 or R4. In an experiment to assess soybean yield enhancement by irrigation at different developmental stages, Korte et al. (1983) reported that yield was sensitive to the increased irrigation, at pod elongation stage (R3–R4) and the seed enlargement stage (R5–R6). In addition, from a greenhouse experiment, Dornbos et al. (1989) concluded that the reduction of soybean seed yield was mainly due to the reduction of seed number than seed size which could cause overall losses under drought stress conditions.

Stem growth habit is an important key factors affecting yield in soybean (Kato et al. 2015). However, yield attributes to growth habit have not been consistent; Kato et al. (2015; Parvez et al. 1989; Robinson and Wilcox 1998) have shown that determinate cultivars out yielded compared to indeterminate growth habit cultivars, while Weaver et al. (1991), have shown on the other way around. The dominance of yield either in determinate or indeterminate cultivars has been suggested to result from other factors including location and genetic background (Ouattara and Weaver 1995; Pfeiffer and Harris 1990). Furthermore, soybean seed yield is related to the number of seed-bearing pods produced per unit area, which also could be related to the number of flowers produced by the plant and the proportion of flowers that develop into pods. The post-flowering phases are often considered as the most critical periods of soybean development, which requires optimum soil moisture for the yield determination (Choi et al. 2016). Recent studies have reported the ability of indeterminate plants to produce more pods and seeds due to a relatively longer flowering period of nodes on the mainstem. Hence, it may be important to elucidate how yield components influence yield formation on a phenotypic level in soybean for better agronomic management decisions.

However, to our knowledge, the differences in pod distribution patterns and canopy yield components based on the stem growth habits in determinate and indeterminate soybean cultivars under progressive soil moisture stress levels have not been reported. Moreover, the functional relationships for modeling are limited and additional studies under realistic solar radiation environments are needed to improve the existing soybean simulation models for field applications. Therefore, the objectives of this study were to evaluate the responses of growth and yield traits including pod distribution patterns, and to identify the agronomic performance of two soybean cultivars based on the growth and reproductive dynamics under variable water-limited conditions for better management decisions.

Materials and methods

Experimental condition and plant materials

This study was conducted utilizing sunlit Soil–Plant–Atmosphere–Research (SPAR) chambers located at the Rodney Foil Plant Science Research facility of Mississippi State University, Mississippi State, MS. These units have the capability to precisely control air temperatures and chamber atmospheric CO_2 concentration at preset set points and at near ambient levels of photosynthetically active radiation (PAR). Each SPAR chamber consists of a 1.27 cm thick Plexiglas which allows 97% of the visible solar radiation to pass without spectral variability in absorption (Zhao et al. 2003). The Plexiglas chamber (2.5 m tall by 2 m long by 1.5 m wide) to accommodate aerial plant parts and a steel soil bin (1 m deep by 2 m long by 0.5 m wide) houses the root system. Air temperature in each SPAR chamber was set to 29/21 °C (day/night) and monitored and adjusted every 10 s throughout the day and night and maintained within ± 0.5 °C of the treatment set points measured with aspirated thermocouples. The daytime temperature was initiated at sunrise and returned to the nighttime temperature 1 h after sunset. The chamber CO_2 concentration was monitored and maintained at 400 μmol mol^{-1} using a dedicated LI-6250 CO_2 analyzer (Li-COR, Inc., Lincoln, NE). The relative humidity of each SPAR unit was monitored and calculated according to the procedure of Murray (1967), with a humidity and temperature sensor (HMV 70Y, Vaisala, Inc., St. Louis, MO) installed in the returning path of airline ducts. To maintain a constant humidity, chilled mixture of ethylene glycol and water was circulated through the cooling coils located outside the air handler of each chamber via several parallel solenoid valves that opened or closed depending on the cooling requirement. Variable density shade cloths (Hummert Seed Co., St. Louis, MO) designed to simulate solar radiation diminution through the plant canopy were placed around the edges of the plant canopy. These were adjusted regularly to match canopy height and to eliminate the need for border plants. In addition, there was a heating and cooling system connected to air ducts that pass conditioned air through the plant canopy to cause leaf flutter. More details of operation and control of the SPAR facility have been described by Reddy et al. (2001). The mean values of day/night temperature, chamber CO_2 concentrations, and vapor pressure deficit (VPD) are provided in Table 1.

Seeds from two soybean cultivars representing the same maturity Group V, having two different growth habits indeterminate type—Asgrow AG5332 and determinate type—Progeny P5333RY were sown in PVC (polyvinylchloride) pots (15.2 cm diameter by 30.5 cm high) with a 500 g of gravel at the bottom of each pot and filled with the soil medium consisting of 3:1 sand: top soil classified as sandy loam (87% sand, 2% clay, and 11% silt). Each pot had a small hole at the bottom for excess water drainage. Initially, all the pots were arranged outside the SPAR units, and when the plants reached R1 stage, pots were moved inside the units. Inside the SPAR units, pots were organized in a completely randomized design with 12 replications per cultivar arranged in six rows with two pots per row. In total, 120 pots were used for the five soil moisture stress treatments. Initially, four seeds were sown in each pot and 6 days after emergence; the plants were thinned to one per pot. Plants were fertigated with full-strength Hoagland's nutrient solution delivered through an automated and computer-controlled drip irrigation system to ensure favorable nutrient and water conditions for plant growth.

Table 1 Treatments based on the percentage of daily evapotranspiration (ET) imposed at 41 days after planting, average soil moisture, mean temperature, chamber CO_2 concentration, vapor pressure deficits (VPD), and evapotranspiration (ET) during the experimental period for each treatment

Treatments	Soil moisture, m^3 m^{-3}	Mean temperature, °C	[CO_2], μmol mol^{-1}	Mean daily VPD, kPa	Mean daily ET, L d^{-1}
100% ET	0.15a[¶]	26.09a	410a	3.5a	15.95a
80% ET	0.14b	26.19a	405a	3.3a	13.80b
60% ET	0.13c	26.48a	408a	4.2a	12.79c
40% ET	0.12d	25.64a	412a	4.0a	8.73d
20% ET	0.11e	25.96a	409a	4.2a	6.54e

[¶]Soil moisture values are averaged for each treatment from 41 to 126 days after planting. Values within a column with different letter are significantly different at $P < 0.05$

Treatments

The treatments included five levels of irrigation, 100, 80, 60, 40, and 20%, which were maintained based on percent evapotranspiration (ET) values recorded on previous day. Treatments were imposed 41 days after planting (DAP) and continued until the harvest, 126 DAP. Each SPAR unit was set at the given soil moisture stress treatment. All treatments were irrigated with the same water volume as in the 100% ET treatment until the time that each treatment was imposed. The ET measured on a ground area basis (L d^{-1}) throughout the treatment period as the rate at which condensate was removed by the cooling coils at 900 s intervals (McKininon and Hodges 1985; Reddy et al. 2001; Timlin et al. 2007) by measuring the mass of water in collecting devices connected to a calibrated pressure transducer. Season-long mean ET values for each treatment are provided in Table 1. The amount of irrigation provided to each treatment was adjusted by changing the duration of irrigation that was based on ET values recorded on the previous day.

Measurements

Soil moisture content and midday leaf water potential (MLWP) measurements

Throughout the experimental period (starting from 41 DAP to 126 DAP), soil moisture contents were monitored using soil moisture sensors (5TM Soil Moisture and Temperature Sensor, Decagon Devices, Inc., Pullman, WA) inserted at a depth of 15 cm in every five random pots of each soil moisture treatment. Midday LWP was measured using a pressure chamber (Soil Moisture Equipment Corp., Santa Barbara, CA, USA) between 1200 and 1400 h as described by Turner (1988), three times after imposing treatments, 48, 61, and 68 days after planting in each water-stressed treatment and in both the cultivars to track plant water status in each water-stressed treatment. The youngest fully expanded leaves from three plants were used to estimate midday LWP in each treatment during the study.

Growth measurements

Plant height was recorded every week beginning from 14 DAP until harvest using four plants per cultivar from the each treatment. The number of nodes on the mainstem was recorded for the same period. From the measurements, change in plant height was calculated and plotted against number of days after treatment. Plants were harvested 126 DAP, and leaves and stems were separated from roots to take individual dry weights. The separated leaves, stems, and roots were placed in an oven and dried at 75 °C for 72 h except for seed, which were air dried to obtain total dry weights (TD).

Quantification of pod distribution and yield component measurements

At harvest (126 DAP), all the plants were sampled and the number of pods on each node position, number of branches formed from the mainstem, and number of pods on each branch were counted to identify the differences in pod distribution patterns. After the measurements, the pods were air dried at room temperature to determine pod dry weights. After threshing with a thresher, seeds were air dried separately for each treatment to take number of seeds (SN), seed yield (SY), 100-seed weight (HSW), and harvest index (HI). Harvest index was calculated and expressed as kg seed dry weight per kg of total dry weight.

Data analysis

The SPAR chambers are identical in design to provide uniform growth conditions (Fleisher et al. 2009). All data collected were analyzed using SAS 9.2 (SAS Institute 2011, Cary, NC) as a completely randomized design with 12 replications. Analysis of variance (ANOVA) was used to determine crop parameter response to soil moisture stress. Means among treatments were compared using least significant difference at $P < 0.05$ probability. The regression analyses were carried out using SigmaPlot version 13 (Systat Software Inc., San Jose, CA). The relationships among the soil moisture content and measured crop parameters were tested for linear and sigmoidal functions, and the best-fit regressions were selected.

Results and discussion

Manipulation of soil moisture stress treatments

The soil moisture content monitored throughout the experimental period by soil moisture sensors was significantly different among various ET-based drought-stressed treatments (Table 1), and this facilitated an accurate control of the five soil moisture stress treatments in the SPAR chambers (Fig. 1). The other environmental variables, such as day and night average temperatures, VPDs, and carbon dioxide concentrations, however, were not significantly different among the soil moisture treatments and cultivars (Table 1). On average, the measured soil moisture content regulated through evapotranspiration-based irrigation showed 0.15 m^3 m^{-3} for

Fig. 1 General overview of the soil–plant–atmosphere–research (SPAR) chambers at Mississippi State University, Mississippi State, MS, USA, used in the current study. The picture was taken when the soybean plants were 60 days old

the control treatment (100% ET), followed by 0.14, 0.13, 0.12, and 0.11 $m^3\ m^{-3}$ for 80, 60, 40, and 20% ET treatments, respectively (Fig. 2a). Similar to soil moisture fluctuations, measured evapotranspiration values also differed significantly among the soil moisture treatments (Fig. 2b). In the study period (41–126 DAP and 85 days of treatment), the total evapotranspiration recorded was 1372 L for 100% ET, 1187 L for 80% ET, 1099 L 60% ET, and 751 L and 562 L 20% ET-based irrigation treatments. During the experiment, the incoming daily solar radiation (285–2800 nm) outside of the SPAR units, measured with a pyranometer (Model 4–8; The Eppley Laboratory Inc., Newport, RI), ranged from 0.7 to 26.6 $MJ\ m^{-2}d^{-1}$ with an average of 16.4 $MJ\ m^{-2}d^{-1}$ (Fig. 2b). The evapotranspiration among the treatments fluctuated with the changes in incoming solar radiation over the growing season. The higher cloud/rain incidences restrained the ability of maintaining a constant ET and hence attenuated the ET in some of the days (Fig. 2b). The evapotranspiration was maximum during first 40 days after treatment (75 DAP)

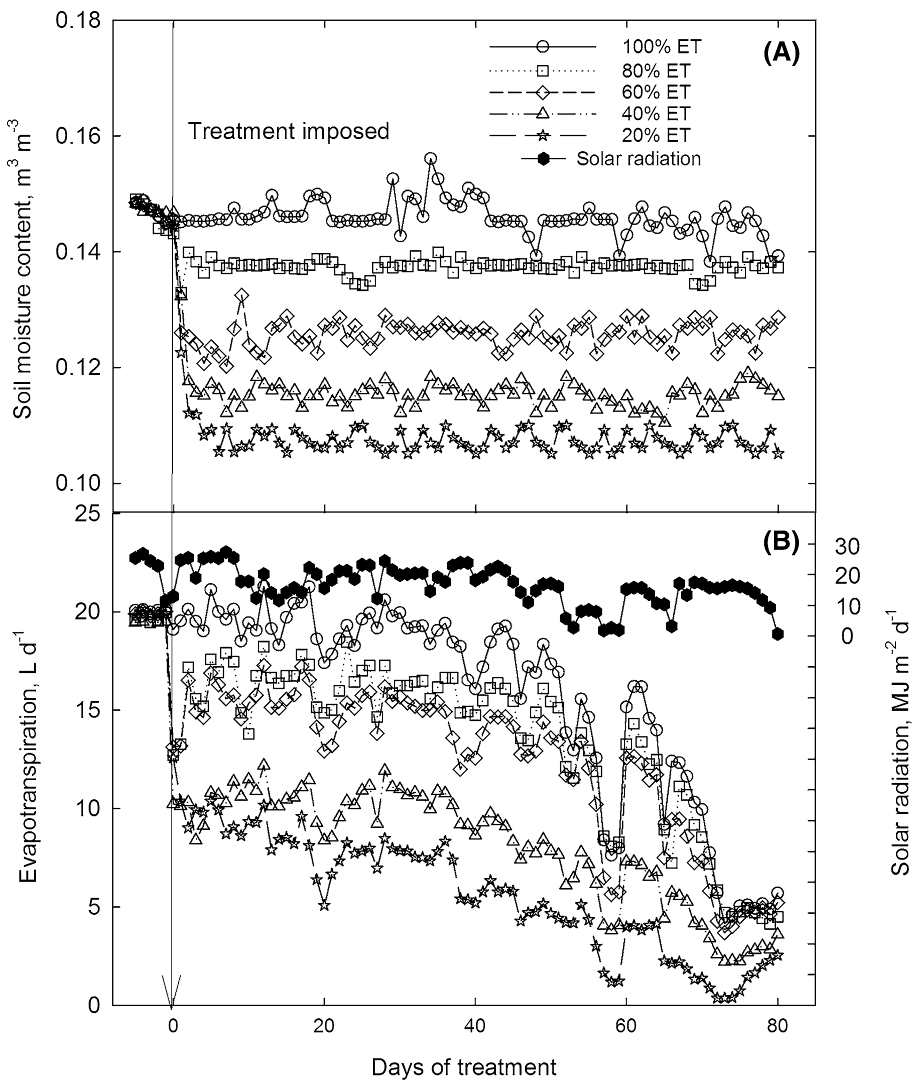

Fig. 2 **a** Volumetric soil moisture content established on evapotranspiration-based irrigation, and **b** daily evapotranspiration and solar radiation across treatments before and during the experimental period. The arrow indicates the day that treatments were imposed and the time when all the soil moisture levels reached the desired treatment levels. Soil moisture values are the average values of five soil moisture sensors at 15 cm depth soil column

due to maximum consumption of water for canopy development and reproductive growth, but decreased afterwards due to plant maturity and shorter day lengths (Fig. 2b). The fluctuations in soil moisture treatments over the treatment period were less compared to fluctuations in ET (Table 1). The midday leaf water potentials (LWP), measured at 48, 61, and 68 DAP, ranged between − 0.90 and − 1.37 MPa across treatments, and increased quadratically with increasing soil moisture content (Fig. 3). Midday LWP, however, was not different between two cultivars within a treatment, but differed among treatments. Midday LWP potential of − 1.0 MPa was achieved at optimum soil moisture content of 0.15 $m^3\ m^{-3}$ soil. In this experiment, a semi-automated ET- and soil moisture sensor-based irrigation under natural solar radiation levels similar to field settings allowed us to develop process-related soil moisture functional algorithms for modeling.

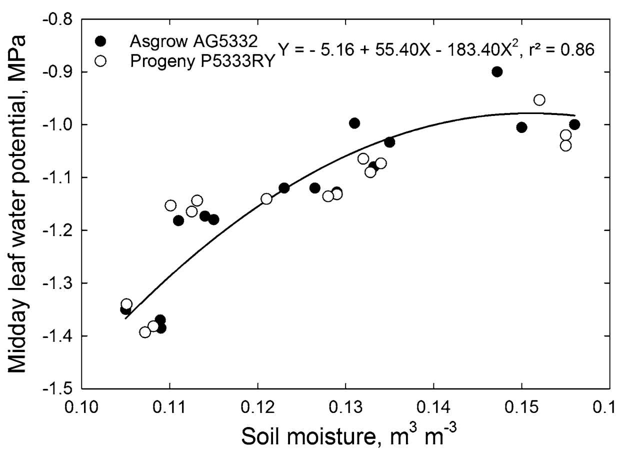

Fig. 3 Relationship between soil moisture content and midday leaf water potential of two soybean cultivars, Asgrow AG5332 and Progeny P5333RY. Each data point is the mean of three measurements taken at 48, 61, and 68 days after planting. The standard errors of means are shown when larger than the symbols. Since there were no differences between the cultivars for midday leaf water potential within a given treatment, a single quadratic function best described the relationship

Growth and developmental attributes

Plant height and node number in both the cultivars showed a significant (Table 2) reduction at very low soil moisture levels (0.12 and 0.11 $m^3\ m^{-3}$) when compared to the control treatment (0.15 $m^3\ m^{-3}$). At 126 DAP, the mean plant height was observed as 104 cm for the control treatment in Asgrow AG5332 cultivar followed by 102, 100, 95, and 79 cm, respectively for 80, 60, 40, and 20% ET treatments. Progeny P5333RY, the determinate type, on the other hand, exhibited shorter plants showing the average plant heights as 86, 85, 84, 76, and 67 cm under 100, 80, 60, 40, and 20% ET treatments, respectively (figures are not shown). The reduction of average plant height for Asgrow AG5332 was 24%, whereas it was reduced by 22% in Progeny P5333RY cultivar, when the soil moisture changed from 0.15 to 0.11 $m^3\ m^{-3}$. The change in plant height, which was calculated each week until harvest, subtracting the corresponding plant height when the treatment was imposed at 35 DAP, was substantially different across the treatments in both the cultivars (Fig. 4). During the first 2 weeks of treatment execution, the change in plant height of Asgrow AG5332 occurred at a slower rate; however, from that point until R5 stage, the change was exponential till it came to a steady state afterwards (Fig. 4a). The determinate type, Progeny P5333RY, reached its maxima 2–3 weeks sooner resulting in shorter plants as compared to the indeterminate Asgrow AG5332 (Fig. 4b). The shorter plants at severe moisture stress levels were attributed to lesser number of mainstem nodes and branches produced similar to other reports (Frederick et al. 2001). The mild (0.13 $m^3\ m^{-3}$) or severe soil moisture stress (0.11 $m^3\ m^{-3}$) reduced the leaf number and leaf size (data not presented) in both the cultivars. Moreover, prolonged soil moisture stress accelerated leaf senescence and led to leaf drop, particularly of mature leaves under higher moisture deficit. Similar soil moisture stress effects on plant height and leaf growth have been observed in previous studies (Lokhande and Reddy 2014). In general, cell division and enlargement were considered to be more sensitive to moisture stress resulting in reduced leaf size, stem elongation, and fewer cells per leaf (Farooq et al. 2009; Khan et al. 2014). Agreeing with the

Table 2 Analysis of variance across soybean cultivars and soil moisture stress treatments and their interactions (cultivar by soil moisture) with soybean morphological and yield parameters measured 126 days after planting; plant height (PH), node number (NN), seed yield (SY), seed number (SN), total dry weight (TDW), biomass partitioning (BMP), and harvest index (HI)

Source of variance	PH	NN	SY	SN	TDW	HI
Soil moisture (Trt)	***	***	***	***	***	***
Soybean (Cul)	**	***	**	NS[¶]	*	***
Trt*Cul	*	*	*	NS	*	***

*, **, ***Represent significant differences at the 0.05, 0.01, and 0.001 *P* level, respectively according to Fisher's LSD

[¶]NS represents nonsignificant differences at the 0.05 *P* level

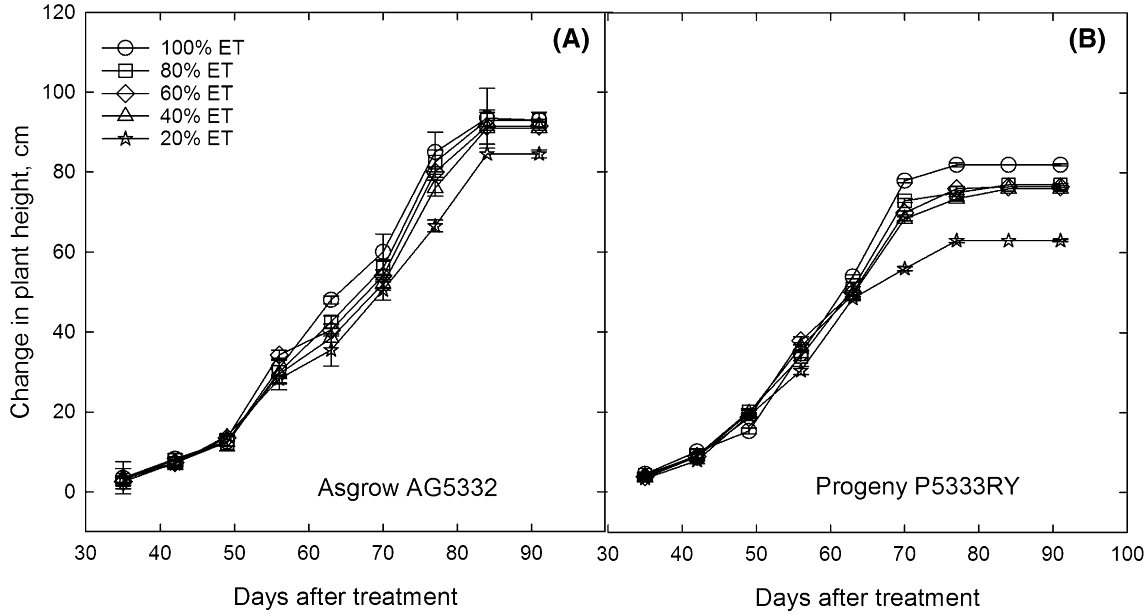

Fig. 4 Time-series analysis of change in plant height in two soybean cultivars, Asgrow AG5332 and Progeny P5333RY, across five soil moisture stress regimes. Symbols represent the observed plant height values subtracting from the corresponding plant height when the treatment was imposed. Each data point is the mean of change in plant height of four individual plants and standard errors of means (SEMS) are shown when larger than the symbols

previous reports, the decrease in vegetative growth could be due to the inhibition of cell elongation by the interruption of water flow from the xylem to the surrounding elongating cells (Anjum et al. 2011), from the reduction in plant photosynthetic efficiency (Farooq et al. 2009), or it might be due to reduction in relative turgidity and dehydration of protoplasm which is accompanied with reduced expansion growth by cell division (Khan et al. 2014).

Yield attributes and pod distribution patterns

In the present study, the pod distribution pattern on the mainstem and branches varied across both cultivars and irrigation levels (Fig. 5). The soil moisture deficit (beyond 60% ET) caused the stressed plants to mature sooner and produced relatively smaller, unfilled pods in both cultivars. A gradual decrease of fertile node number and branch number was observed for both the cultivars when increasing the stress and the lowest yield was obtained from 20% ET treatment (0.11 $m^3\ m^{-3}$). Numerous studies have shown that soil moisture stress imposed during the reproductive stages of soybeans can decrease number of flowers, pods, and seeds (Brevedan and Egli 2003; de Souza et al. 1997; Westgate and Peterson 1993). Soybean yield is principally a function of seeds per unit area, which determines by the number of pods and nodes per unit area (Egli and Yu 1991; Orlowski et al. 2016). The number of pods per plant is considered as the yield component that is most responsible for a higher yield compensation of soybean associated with greater mainstem node and branch development (Board and Modali 2005; Federick et al. 2001; Kahlon et al. 2011).

Mainstem and branch pod number and distribution

Soil moisture stress had a large effect on mainstem and branch pod distribution (Fig. 6). Averaged within the treatments, the middle portion (nodes 8–15) of the canopy of both cultivars contributed more number of pods than the bottom (nodes 1–7) or top (nodes 16+) regions (Table 3). In Asgrow AG5332, pods were distributed from node 4–23 (Fig. 6a) on the mainstem, while, in Progeny P5333RY, the distribution was observed from 5 to 17 nodes (Fig. 6b). The input from the bottom canopy region (nodes 1–7) to the total mainstem pod number was significantly greater (Table 3) in Progeny P5333RY cultivar compared with the bottom region of Asgrow AG5332. In contrast, the top canopy region (nodes 16+) of the Asgrow AG5332 added more number of pods towards the total mainstem pods than Progeny P5333RY. Comparatively, a higher number of mainstem pods on the top region in Asgrow AG5332 might have been continuous addition nodes on the top region due to its indeterminate growth habit. The input from the middle canopy region was significantly higher in Progeny P5333RY (Table 3). For Asgrow AG5332, the input was 55 and 62%, under control and 20% ET, while, under the same treatments, Progeny P5333RY added 69 and 76% contribution to the

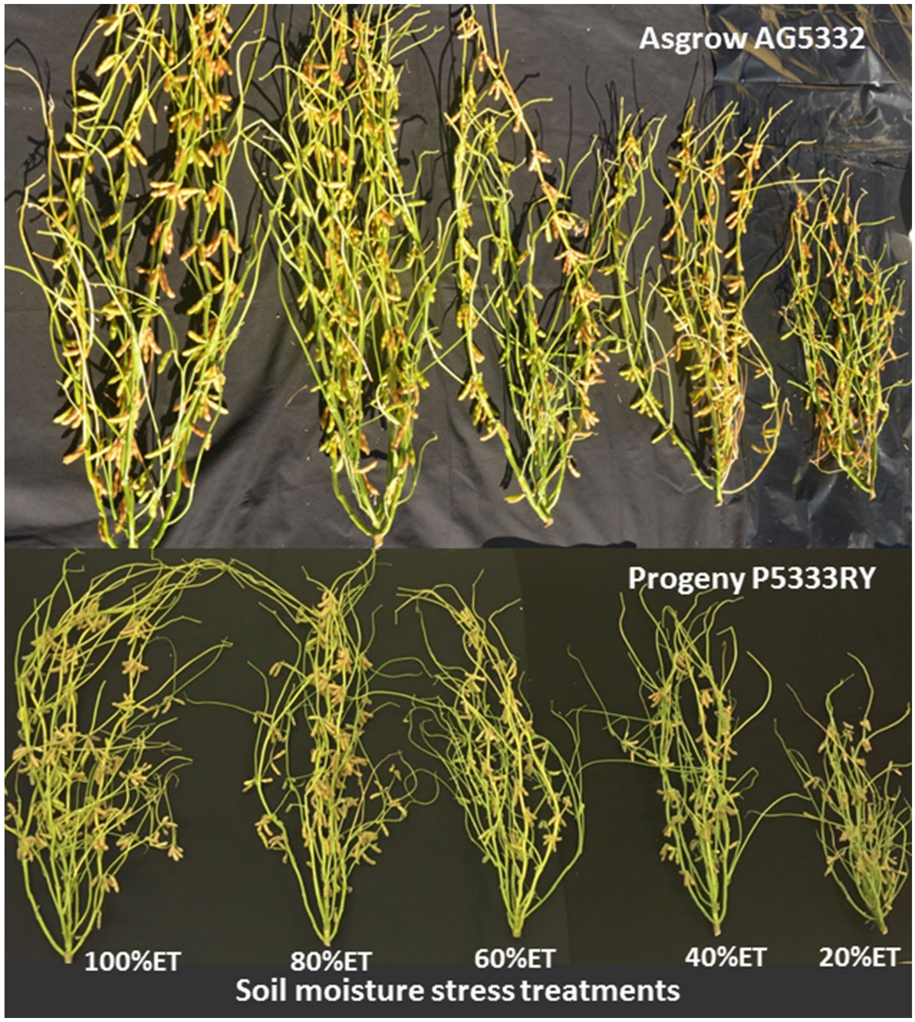

Fig. 5 Pictorial representation of pod distribution patterns of two soybean cultivars harvested 126 days after planting. The average soil moisture conditions for five levels of ET-based irrigation system from left to right 100, 80, 60, 40, and 20% are given as 0.15, 0.14, 0.13, 0.12, and 0.11 $m^3 m^{-3}$. The top and bottom images represent Asgrow AG5332 and Progeny P5333RY, correspondingly

total pods from the middle of the canopy. The variation of the pod numbers in the middle canopy region seemed to be primarily due to the flowering pattern in the determinate type (Progeny P5333RY). This result suggests that determinate growth habit has a direct effect on the formation of more number of pods in the middle canopy region, whereas indeterminate growth habit has a greater influence for the formation of greater number of mainstem pods on the top canopy region.

Branch pod number exhibited a quadratic decline with increasing the branch number from bottom to top on the mainstem (Fig. 6c). The pod yield compensation from the branches formed from first four branches was almost 80 and 85% for Asgrow AG5332 (Fig. 6c) and Progeny P5333RY (Fig. 6d) cultivars, while it was reduced to 81 and 84% under severe water deficit respectively. In accordance with the previous findings (Board 1987), branch pod yield was greater compared to the pod yield on the mainstem and it was about thrice as high as mainstem pod yield. Thus, increasing soybean branching would potentially lead to increased soybean yield even under stressful environments. Averaged over the treatments, branch pod yield of Asgrow AG5332 and Progeny P5333RY grown with 100% ET-based irrigation was 49 and 50% higher than the branch pod yield of soybean under severe moisture stress (0.11 $m^3 m^{-3}$). For the same treatment conditions, pod yield on the mainstem in Asgrow AG5332 and Progeny P5333RY was 35 and 40% greater than the pod yield on the mainstem under 20% ET (0.11 $m^3 m^{-3}$). This endorses the previous findings that soil moisture stress had apparent effect on the vegetative and reproductive growth of the branches, increasing the branch pod yield with optimum moisture content. Therefore, branch seed yield was more sensitive to water stress conditions than mainstem pod yield (Board et al. 1990; Frederick et al. 2001). With respect to 100% ET treatment, the contribution of branch pod yield to total pod yield was 76% in Asgrow AG5332 and 73% in Progeny P5333RY (Table 3). The number of total pods produced on the branches was 108 and 96 under 20% ET treatment for Asgrow AG5332 and Progeny P5333RY cultivars correspondingly (Table 3). Branch pod number

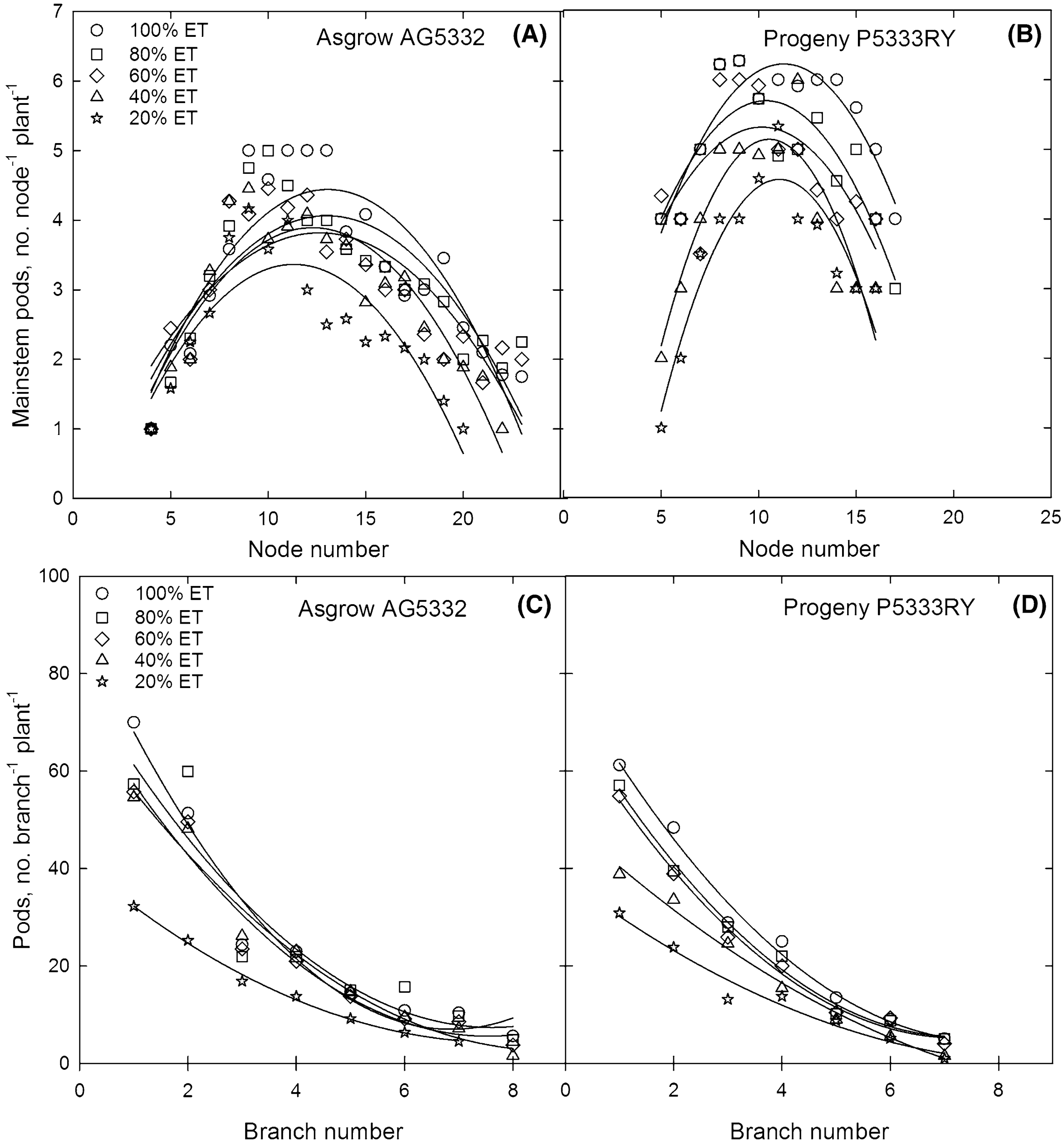

Fig. 6 Soil moisture stress effects on mainstem and branch pod number of Asgrow AG5332 (**a** and **c**) and Progeny P5333RY (**b** and **d**) soybean cultivars harvested 126 days after planting. Each data point is the average of 12 individual plants and standard errors of means (SEMS) are shown when larger than the symbols. The solid lines represent the quadratic regression functions for the given response across each soil moisture stress treatment

of both the cultivars under mild water stress (60 and 40% ET) exhibited a significant reduction compared with control treatment where Asgrow AG5332 had a higher pod number (185 pods plant^{-1}) than for Progeny P5333RY (128 pods plant^{-1}). Some studies have shown that the major fraction of pods and seed yield were found on the branches as compared to the portion coming from the mainstem, and reported that branch seed yield was about twice as high as mainstem seed yield (Board 1987). As reported in the previous studies, even though the mainstem yield is relatively stable across the environments (Federick et al. 2001), branch yield has been reported to be controlled by both genetics (Nelson 1996) and environmental factors such as soil moisture stress (Board et al. 1990; Federick et al. 2001).

Seed number

The seed number exhibited a quadratic decline with increasing the soil moisture stress (Fig. 7). The results of analysis of variance show that the two soybean cultivars

Table 3 Yield potential of two soybean cultivars based on the canopy region

Cultivar	Soil moisture (m^3 m^{-3})	Pod numbers in each canopy region (corresponding node, no. $plant^{-1}$)			Total mainstem pods, no. $plant^{-1}$	Total branch pods, no. $plant^{-1}$	Total pods, no. $plant^{-1}$
		Bottom (1–7)	Middle (8–15)	Top (16+)			
Asgrow AG5332	0.15	8a[¶] (12%)	36a (55%)	21a* (32%)	65a (24%)	210a* (76%)	275a*
	0.14	8a (13%)	33b (53%)	21a* (34%)	62a (23%)	206a* (77%)	268a*
	0.13	8a (14%)	32b (54%)	19ab* (32%)	59b (24%)	185b* (76%)	244b*
	0.12	8a (15%)	31b (57%)	15b* (28%)	54b (23%)	185b* (77%)	239b*
	0.11	8a (19%)	26c (62%)	9c* (21%)	42c (28%)	108c* (72%)	150c*
Progeny P5333RY	0.15	13a* (19%)	48a* (69%)	9a (13%)	70a (27%)	191a (73%)	261a
	0.14	13a* (21%)	43b* (68%)	7a (11%)	63b (27%)	170b (73%)	234b
	0.13	12a* (21%)	41b* (73%)	4b (7%)	56c (34%)	163b (74%)	220c
	0.12	9b (19%)	36c* (75%)	3c (6%)	48d (27%)	128d (72%)	176d
	0.11	7c (17%)	32d* (76%)	3c (7%)	42d (30%)	96e (70%)	138e

The pods from the mainstem nodes were divided in to three main subsections as bottom (node 1–7), middle (node 8–15), and top (node 16+). The mean total pods from the mainstem and branches and the average total pods per each plant were given accordingly as influenced by different soil moisture stress treatments

[¶]Different lower case letters within a column are significantly different at $P < 0.05$ and compare the soil moisture stress effects on pod number. Among the subsections, the percent value followed by the lower case letter represents the percent contribution of each canopy region to the total mainstem pod number. In addition, for the each soil moisture stress treatment, the percent contribution form mainstem and branch pod to the total number of pods is given within the parenthesis. The asterisk within a column compares the main effect between the cultivars for pod number and denoted as * when the values are significantly higher than the other cultivar at $P < 0.05$

were not significantly different for seed number (Table 2). Means comparison has shown that Asgrow AG5332 with 275 pods had the highest number of seeds (504 seed $plant^{-1}$) per plant compared to Progeny P5333RY with 261 pods and 494 seeds per plant under control conditions (Fig. 7). When the soil moisture varied from 0.15 to 0.11 m^3 m^{-3}, the total seed number was reduced by 46 and 44% for Asgrow AG5332 and Progeny P5333RY, respectively. This reduction in seed number may be due to the production of fewer pods per plant under stressed condition. Previous studies have shown the importance of having a large number of seeds per unit area to acquire a high soybean yield. Pod number per plant, number of seeds per pod, and seed mass affected soybean seed yield and these traits are the most important components, which determine an improved soybean yield. Soil moisture stress during seed-filling stage leads to the largest reduction in seed number due to the shortening of the duration of seed fill (Board 1987; Brevedan and Egli 2003).

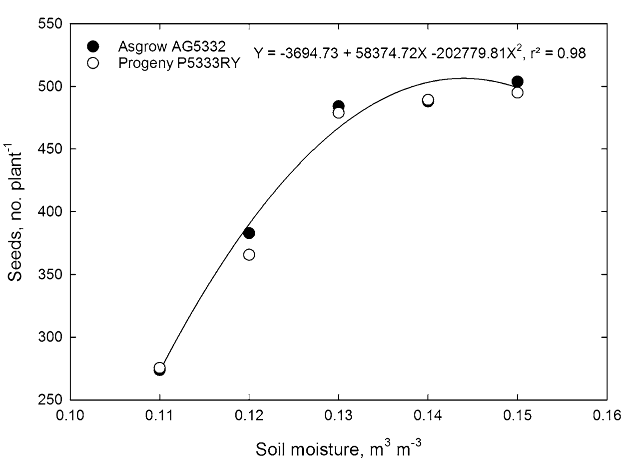

Fig. 7 Soil moisture stress effects on average seed number of Asgrow AG5332 and Progeny P5333RY soybean cultivars harvested 126 days after planting. Each data point is the average of 12 individual plants and standard errors of means (SEMS) are shown when larger than the symbols

Mainstem and branch pod dry weight

By consistent with mainstem pod number, mainstem pod dry weight also revealed sigmoidal responses against the node number for both Asgrow AG5332 (Fig. 8a) and Progeny P5333RY (Fig. 8b). Pods located in the middle canopy contained greater dry weight than the pods positioned on the top or bottom regions. The treatment effect was substantial for the mainstem pod dry weight where a significant reduction of mainstem pod dry weight was observed under severe moisture stress (0.11 m^3 m^{-3}) compared to control and mild water stresses. Branch pod dry weight responses to soil moisture stress were similar to those of branch pod yield (Fig. 8c, d). The pods on the first four branches had the highest dry weight for both the cultivars where it decreased significantly when the moisture stress changed from optimum to severe.

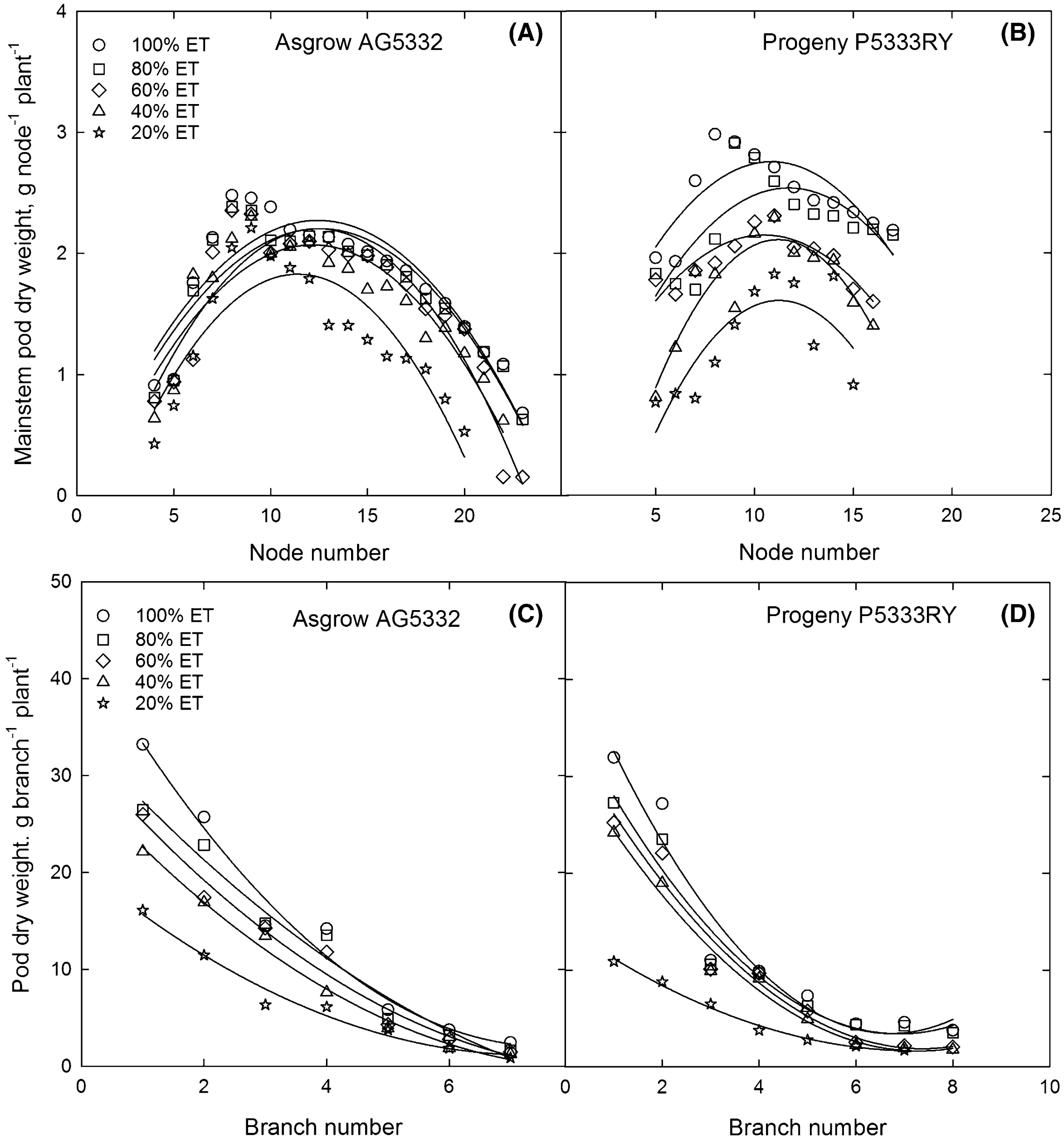

Fig. 8 Soil moisture stress effects on mainstem and branch pod dry weight of Asgrow AG5332 (**a** and **c**) and Progeny P5333RY (**b** and **d**) soybean cultivars harvested 126 days after planting. Each data point is the average of 12 individual plants and standard errors of means (SEMS) are shown when larger than the symbols. The solid lines represent the quadratic regression functions for the given response across each soil moisture stress treatment

Total weight, seed yield, and harvest index

The total dry weight of soybean plants exposed to moderate-to-severe soil moisture stress was significantly less than their controls both in Asgrow AG5332 and Progeny P5333RY (Fig. 9a). The decline of total dry matter under 0.11 $m^3\ m^{-3}$ moisture content compared to the control was 43% in Asgrow AG5332 and 54% in Progeny P5333RY. Both cultivars exhibited a quadratic decline in total dry matter with respect to increasing soil moisture stress. There was a significant difference among the treatments for seed weight (Fig. 9b), 100-seed weight (HSW) per plant, and harvest index (Fig. 9c) when the soil moisture varied from control to severe stress. For indeterminate Asgrow AG5332, HSW was 19 and 12 g per 100 seeds under 100 and 20% ET, while, under same treatment conditions, Progeny P5333RY exhibited 17 and 12 g per 100 seeds (data not shown). 50 and 64% for Asgrow AG5332 and Progeny P5333RY cultivars reduced the seed yield, respectively, when the soil moisture content varied from

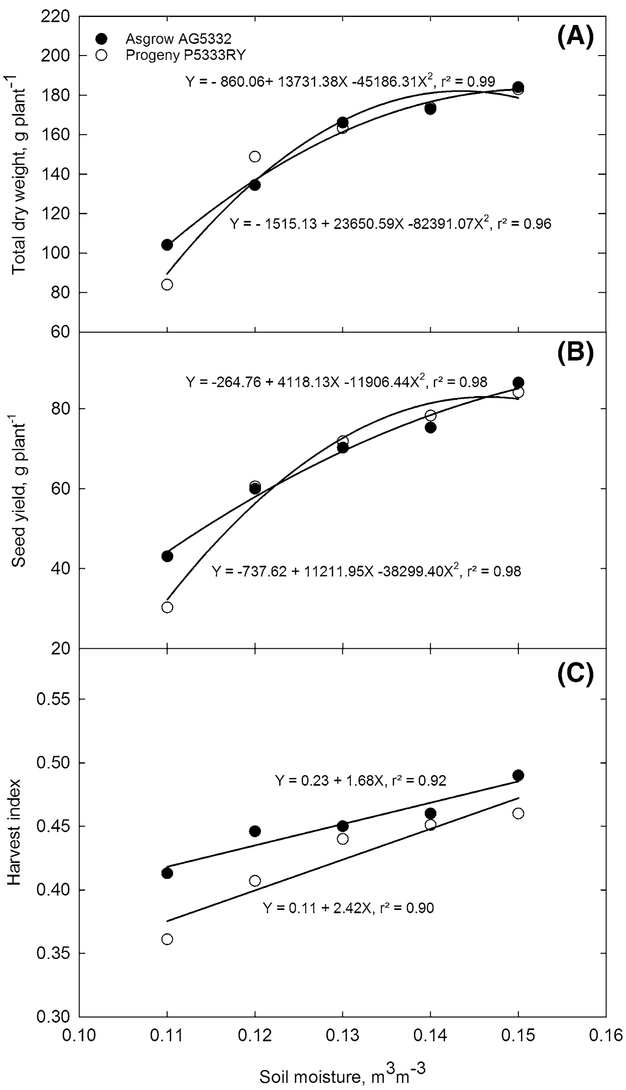

Fig. 9 Soil moisture stress effects on **a** total dry weight, **b** seed yield, and **c** harvest index of Asgrow AG5332 and Progeny P5333RY soybean cultivars harvested 126 days after planting. Each data point is the average of 12 individual plants and standard errors of means (SEMS) are shown when larger than the symbols

optimum to severe moisture stress (Fig. 9b). In general, seed yield is a result of the rate and duration of effective seed-filling period; hence, this finding implies that the decrease of seed yield under stress conditions might be due to the disruption of carboxylation and remobilization of photosynthetic products during reproductive growth stages resulting in pod and seed abortion. The average weight of seeds decreased with increasing the soil moisture stress resulting in an increased number of small-shriveled seeds in the seed lot. From the previous studies, it was well established that the reduction of seed size is due to the shortening of the seed-filling duration rather than affecting seed growth rate under water deficit.

Similar to seed yield, harvest index [defined as dry seed weight (kg) per total weight (kg)] also showed a significant difference among the cultivars and within the treatments (Fig. 9c). It declined linearly in both the cultivars where the decline was steeper in Progeny P5333RY than in Asgrow AG5332. The harvest indices decreased by 16 and 21%, when the soil moisture content varied from control to severe stress. Overall, under both control (100% ET) and 20% ET level (0.11 m^3 m^{-3}), Asgrow AG5332 has shown higher values for pod number, seed number, seed dry weight, and harvest index compared to the Progeny P5333RY. These results suggest that the indeterminate stem growth habit directly has a positive effect on the yield attributes. Typically, nodes on the mainstem of indeterminate type soybean continue to differentiate even after onset of flowering, resulting in an increase of nodes. On the other hand, determinate types cease vegetative activity at or soon after photoperiod-induced floral induction; hence, the number of nodes is likely to be considerably small (Tian et al. 2010). The large number of nodes and branches on the mainstem may have caused the large number of pods and seeds per plant of indeterminate type Asgrow AG5332 in the present study. Since stem termination has great effects on plant height, flowering period, node production, and maturity, indeterminate types with prominent genetic background might be much advantageous to attain stable and improved yield potential under water-stressed conditions.

Biomass partitioning

Soil moisture stress treatments significantly affected biomass partitioning among plant components at the harvest (Fig. 10). Averaged across soil moisture stress treatments, the biomass partitioning to stem and root increased by 9 and 12% in Asgrow AG5332 under severe water deficit, while leaf and seed decreased by 30 and 17% compared to the control treatment (Fig. 10a). For Progeny P5333RY, leaf and seed partitioning decreased by 27 and 22%, whereas stem and root partitioning was increased by 27 and 45% (Fig. 10b), respectively. This indicates that the soil moisture stress imposed at reproductive stage increased the average biomass partitioning to stem and roots, while partitioning to leaves and seeds was drastically reduced for both cultivars. The allocation of nutrients and biomass partitioning among different plant organs revealed the plant's capability to adjust physiological and metabolic processes under the given environmental condition. By increasing the biomass partitioning to the roots, it promotes efficient uptake of water and nutrients in an effort to enhance carbon assimilation under moisture stress condition. As reported in the previous studies, soil moisture stress inhibits the dry matter production mainly through its inhibitory effects on leaf development, leaf area expansion, and, subsequently, reduced light interception (Nam et al. 1998). Yield

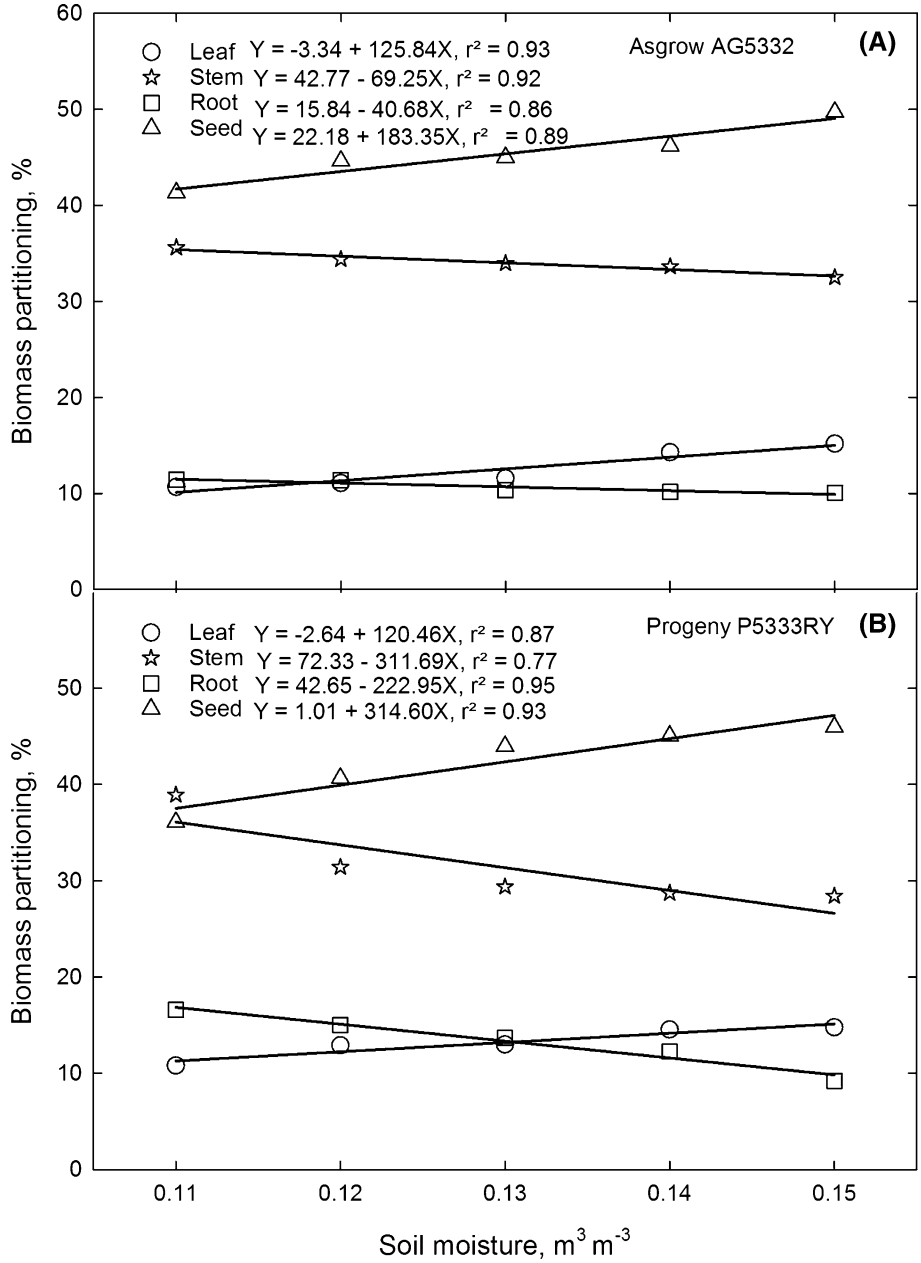

Fig. 10 Soil moisture stress effects on biomass partitioning of Asgrow AG5332 and Progeny P5333RY soybean cultivars harvested 126 days after planting. The different open symbols represent the percent biomass partitioning to the leaf, stem, root, and seed under different soil moisture treatments, respectively. Each data point is the average of 12 individual plants and standard errors of means (SEMS) are shown when larger than the symbols

is a function of the amount of radiation intercepted, carbon assimilation through canopy photosynthesis, and the percentage of this assimilates allocated to yield components. Hence, reduced partitioning towards yield-related traits such as pods and seeds contributed to a larger decline in yield under severe moisture deficiency.

Conclusion

In this study, we compared two soybean cultivars having two different growth habits for yield components and pod distribution patterns. Our results indicate that the two soybean cultivars have marked variations in plant growth characters: yield and yield attributes under soil moisture deficit. Extended soil moisture stress during reproductive growth accelerated leaf senescence and led to leaf drop particularly mature leaves under higher moisture deficit treatments. Asgrow AG5332, the indeterminate type, exhibited taller stems and more nodes than determinate Progeny P5333RY cultivar. Differences in mainstem and branch yield components were observed among the cultivars under soil moisture stress treatments. For both the cultivars, the middle portion of the canopy contributed a larger number of pods than the bottom or top regions and determinate growth habit had a large effect on the formation of more number of pods in the middle canopy region than indeterminate growth habit. Branch pod yield was greater in both the cultivars compared to the pod yield on the mainstem and it was about threefold as high as mainstem pod yield. Therefore, the production of more branches per plant could potentially increase the yield. However, branch pod yield was more susceptible to soil moisture stress compared to mainstem yield, suggesting that water stress occurring at reproductive stage reduces soybean yield principally by reducing branch growth, which results in fewer branch pods and seed yield. Asgrow AG5332 has shown greater yields due to increased node, pod, and seed number, seed dry weight, and seed production efficiency compared to the Progeny P5333RY. The identified soil moisture and plant processes-dependent functional algorithms will be useful to improve the existing soybean simulation models (Battisti and Sentelhas 2015; Keating et al. 2003; Nendel et al. 2011), which could be used for field management. Cultivar selection for high yield potential and yield characteristics may lead to faster cultivar improvement in the breeding for high yielding varieties and could be advantageous for the soybean producers for the adoption of best management practices aiming to increase seed yield.

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