Field Crops Research 216 (2018) 209–216

Contents lists available at ScienceDirect

Field Crops Research

journal homepage: www.elsevier.com/locate/fcr

Physiological activity and biomass production in crop canopy under a tropical environment in soybean cultivars with temperate and tropical origins

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ARTICLE INFO

Keywords:
Canopy temperature
Soybean
Transpiration
Tropical environment

ABSTRACT

In order to explore the plant factors facilitating better adaptation of soybean to high temperatures, genotypic variability till the beginning of seed filling (R5) were examined with reference to biomass production, relative transpiration activity and relevant plant factors under a tropical environment. Twenty-nine (in 2014 and 2015) and 20 (in 2016) soybean cultivars of temperate (Japan and USA) and tropical (Indonesia-old, Indonesia-modern, and Others) origin were grown in Serang, Banten (2014 and 2015; Experiment 1) and in Bogor, West Java (2016; Experiment 2), Indonesia. In Experiment 1, aboveground biomass at R5 (TDW_{R5}) of the temperate cultivars was one-third to one-fourth of that of the tropical cultivars. This was associated with less than half the amount of the cumulative intercepted radiation to R5 (CIR_{R5}) due to their shorter growth duration and lower value of the mean fraction of canopy light interception till R5 (mean $F_{VE\text{-}R5}$). In addition, the radiation use efficiency (RUE) at R5 of the temperate cultivars was also as low as 0.54 g MJ^{-1}, as compared to 0.87 g MJ^{-1} in the tropical cultivars. The value of canopy temperature minus air temperature (CTd), as an indicator of relative transpiration activity, of temperate cultivars was markedly larger than that of the tropical cultivars, indicating lower transpiration activity in temperate cultivars, which was associated with the low RUE. In Experiment 2, greater activity of transpiration in tropical cultivars was attributed to their higher stomatal conductance (g_s) and greater stomatal density (N_{stoma}) of upper leaves than that in those from the temperate regions. These results indicate that low biomass production in temperate cultivars occurs not only due to the cumulative intercepted radiation in the canopy but also due to low RUE and that the low RUE in temperate cultivars is associated with low gas exchange activity, in which leaf morphological traits are involved. Within temperate cultivars, US cultivars tended to perform better than the Japanese cultivars with respect to gas exchange activity.

1. Introduction

Soybean [*Glycine max* (L.) Merr.] is one of the most important crops globally, and is used often as protein meal and vegetable oil. Worldwide, the total area supporting soybean production has expanded more rapidly than that of any other major crop since the 1970s, increasing from 29.5 million ha in 1970–117.5 million ha in 2014 (Food and Agriculture Organization, 2017), in response to growing global demand for soybean products over the past four decades. Soybean production is largely predominant in temperate regions due to cool to moderately warm climates, with the USA, Brazil, and Argentina accounting for 84% of the world's harvest in 2014. Expanding soybean production to the tropical regions represents a possible means for increasing global soybean production in order to meet soaring consumer demand; soybean cultivation in the warmer and wetter climates of the tropics represent numerous challenges, however. Soybean production in relatively high-temperature environments has also increased throughout temperate regions due to climate change and global warming, and increasing of global surface temperatures will have significant impacts on soybean production (Prasad et al., 2006), especially

Abbreviations: CIR_{R5}, cumulative intercepted radiation to R5; CTd, canopy temperature minus air temperature; *F*, fraction of radiation intercepted; $F_{VE\text{-}4WAP}$, *F* from seedling emergence to four weeks after planting; $F_{VE\text{-}R5}$, F from seedling emergence to R5; g_s, stomatal conductance; L_{guard}, guard cell length; L_{vein}, total leaf venation; N_{epi}, epidermal cell density; N_{stoma}, stomatal density; RUE, radiation use efficiency; SI, stomatal index; TDW_{R5}, aboveground biomass at R5; Δ, carbon isotope discrimination

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https://doi.org/10.1016/j.fcr.2017.11.012
Received 21 August 2017; Received in revised form 13 November 2017; Accepted 13 November 2017
0378-4290/

in those tropical regions where current climatic conditions and temperatures are close to optimum for soybean growth, for which further temperature increase will reduce yields (Prasad et al., 2017).

The effects of higher ambient temperatures on soybean have been studied extensively under both, field and controlled laboratory conditions, and indirectly through the construction of model simulations (Tacarindua et al., 2012, 2013; Kumagai and Sameshima, 2014; Kantolic et al., 2013; Kantolic and Slafer, 2001; Wu et al., 2015; Setiyono et al., 2007, 2010). Tacarindua et al. (2012, 2013), for instance demonstrated that elevated temperature had a significant negative effect on soybean performance in a temperature gradient chamber (TGC), with slower growth rate resulting in reduced yield and biomass. Moreover, it has been shown that higher temperatures alter plant phenology and hasten flowering onset (Han et al., 2006; Wu et al., 2015; Kantolic and Slafer, 2005, 2007; Setiyono et al., 2007, 2010; Gaynor et al., 2011), enhance plant development (Craufurd and Wheeler, 2009), and in some cases, prolong the seed filling period (Tacarindua et al., 2013; Thomas et al., 2010). High temperatures effect on soybean also result in smaller seed size (Tacarindua et al., 2013; Thomas et al., 2010), increase seed shriveling (Tacarindua et al., 2013; Thomas et al., 2010; Smith et al., 2008; Bellaloui et al., 2017), and reduce nutritional quality (Smith et al., 2008; Bellaloui et al., 2017) and seed germination and vigor (Chebrolu et al., 2016; Smith et al., 2008; Bellaloui et al., 2017). Although the effects of temperature on yield and growth performance of soybean are well documented, less is known about the role of genetic variability in soybean responsiveness to high temperature (Mochizuki et al., 2005; Chebrolu et al., 2016) and, whether cultivars adapted to temperate and tropical regions differ in their adaptation to warm climates.

Tropical environments are characterized by relatively warm temperatures and constant day-length (time from sunrise to sunset) throughout the year. Monthly mean air temperatures in the tropics range between 20 and 30 °C and the difference in mean temperatures between cool and hot months is typically less than 7 °C (Monteith, 1977). In the tropics, the day-length is just over 12 h at the equator as against 10.6–13.7 h at 25° latitude. Such environmental conditions are typical in Indonesia, thus making the country an ideal location for studying the growth, development, and physiological aspects of soybean for adaptation to future climate change.

In a previous study, we had shown that the yield and seed quality of temperate cultivars grown in tropical environments were lower than those of tropical cultivars even after differences in growth duration were taken into account (Saryoko et al., 2017). We also found that harvest index between the temperate and the tropical groups did not differ considerably, indicating that the process of biomass production may be involved in these differences. The objective of the present study was to assess the role of genotypic variability among soybean cultivars originating from temperate and tropical regions with respect to crop physiological activity and biomass production, relative transpiration activity, and its associated factors under a tropical environment.

2. Material and methods

2.1. Experiment 1

Twenty-nine soybean cultivars were grown from July–November 2014 and from March–July 2015 at the AIAT Banten Research Station in Serang, Banten Province, Indonesia (lat. 6.1°S, long. 106.2°E). The cultivars were divided into five groups based on the region of their origin, which consisted of Japan and USA (temperate cultivars), and Indonesia-old, Indonesia-modern, and Others (tropical cultivars); the cultivars are listed in Table 1. Cultivars were selected on the basis of region, maturing traits, and representativeness of commercial cultivars. Seeds were sown in 2.4 m × 2 m plots on July 19, 2014 and were arranged in a spacing of 50 × 20 cm, and on March 17, 2015 in a spacing of 40 × 20 cm, with three replicates. Plants were thinned after seedling emergence, leaving one plant per hole. Plot soils were fertilized with N (5 g m^{-2}), P_2O_5 (2.7 g m^{-2}) and K_2O (7.5 g m^{-2}) in the form of urea, calcium superphosphate, and potassium chloride, respectively. Irrigation and pest control regimes were based on regional management programs in order to optimize growth conditions. Daily air temperatures were measured with a HMP45C temperature sensor (Campbell Scientific, INC., Logan, UT), and the incident solar radiation was measured using a CMP3 pyranometer (Kipp and Zonen, B.V., The Netherlands) and recorded with a CR1000 datalogger (Campbell Scientific, Inc., Logan, UT).

Table 1
Name, origin and classification of regions of soybean cultivars for Experiment 1 and 2.

Group of origin (n)	Cultivar name	region
Japan (n = 5)	Enrei, PI416937, Tanbaguro, Tachinagaha and Fukuyutaka	Temperate
USA (n = 5)	UA4805, DS24-2, DS25-1, DS34-3 and DS65-4	Temperate
Indonesia-old (n = 5)	Merapi, Tidar, Ringgit, Wilis and Local Tegineneng	Tropics
Indonesia-modern (n = 5 or n = 2)	Dering-1, M100-47-52-13†), M150-7B-41-10†), Tanggamus and SC-1-8†)	Tropics
Other tropical (n = 9 or n = 3)	MANSHUU MASSHOKUTOU†), ICHIGUUHOU†), N 2491, M 652†), SAN SAI†), SJ4, SANDEK SIENG, E C 112828†) and MISS 33 DIXI†)	Tropics

Cultivar name followed by symbol (†) was excluded for Experiment 2.

Plant developmental stages were recorded following the protocol described by Fehr and Caviness (1977). At the early seed filling stage (R5), six plants were collected per plot and oven dried at 80 °C for 48 h to measure the aboveground biomass (TDW_{R5}). Canopy development was expressed as the mean value of the fraction of radiation intercepted (F). The values of F were estimated weekly from light intercepted above the canopy using a digital imaging technique (Purcell, 2000; Shiraiwa et al., 2011; Bajgain et al., 2015; Kawasaki et al., 2016), following which the daily fraction of solar radiation was estimated by interpolation and its mean was calculated. The speed of canopy development was calculated as the mean F over the period from seedling emergence until four weeks after planting (WAP, mean $F_{VE\text{-}4WAP}$). Canopy size at R5 was determined as the mean F from seedling emergence to onset of R5 (mean $F_{VE\text{-}R5}$). The accumulated incident solar radiation from seedling emergence to R5 was derived from daily local meteorological data. The cumulative intercepted solar radiation to R5 (CIR_{R5}) was calculated by multiplying the mean daily incident solar radiation (SR) with the mean $F_{VE\text{-}R5}$:

$$CIR_{R5}\ (\mathrm{MJ\ m^{-2}}) = SR \times \text{mean}\ F_{VE\text{-}R5} \quad (1)$$

Energy utilization efficiency was estimated as radiation use efficiency (RUE) until onset of the R5 stage. The RUE was calculated as total biomass produced until the R5 stage per cumulative intercepted radiation:

$$RUE\ (\mathrm{g\ MJ^{-1}}) = TDW_{R5}/CIR_{R5} \quad (2)$$

Digital images of the canopy were captured with an infrared camera (Thermo Gear G100EX, Nippon Avionics, Japan) three times daily (around 10 AM, 11:30 AM, and 1 PM) three days a week at six WAP (Supplemental 1). Infrec Analyzer software (Nippon Avionics, Japan) was used to estimate canopy temperature (CT) from the digital images. Canopy temperature minus air temperature (CTd) was calculated as the difference between CT and air temperature (AT) at the time of the measurements:

$$CTd\ (°C) = CT - AT \quad (3)$$