Photosynthetic and transpiration rates of soybean as affected by different irradiances during growth

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Abstract

The diurnal variation of net photosynthetic (P_N) and transpiration (E) rates in soybean [*Glycine max* (L.) Merr. cv. Fukuyutaka] plants grown under 100, 50, or 25 % of full sun irradiance (I_{100}, I_{50}, I_{25} plants) were compared. In the morning, activities of the plants were measured at irradiances under which they grew. However, during the afternoon, all the plants were tested under full irradiance. The lower the growth irradiance, the lower P_N, E, and mesophyll conductance values were found. Stomatal conductance was considerably lower in I_{25} plants only. Both the increase in specific leaf area (SLA) and the decrease in nitrogen content per leaf area unit contributed to the P_N reduction of soybean plants grown under low irradiances. Though E of the plants grown under different irradiances differed less markedly than P_N, the water use efficiency declined from I_{100} to I_{25}.

Additional key words: *Glycine max*; growth; leaf nitrogen content; mesophyll conductance; specific leaf area; stomatal conductance.

Introduction

Different plant population densities create a different environment within the canopy, especially a different distribution of sun radiation. A higher canopy density results in increasing LAI as well as increasing radiation interception by the top of the canopy (Sakamoto and Shaw 1967a, Isoda *et al.* 1992). Consequently, P_N declines from top to bottom of the canopy according to the irradiance of individual layers of leaves (Monsi and Saeki 1953, Sakamoto and Shaw 1967b, Monteith 1981).

There were two main purposes of the described research: (*1*) to characterize the diurnal changes of P_N and E in soybean plants grown under different irradiances simulating the situation within soybean canopies of different densities, and (*2*) to determine the factors responsible for these differences in P_N and E.

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Materials and methods

The determinate soybean [*Glycine max* (L.) Merr. cv. Fukuyutaka] was grown in 8 000 cm^3 pots at experimental farm of the College of Agriculture, Ehime University, Matsuyama. Prior to planting, a fertilizer composed of 0.3 g N, 0.6 g P_2O_5, 0.6 g K_2O, and lime was applied on soil of each pot. On June 30, 1995, three seeds per pot were sown. Two weeks afterwards only one plant per pot was left. After further four weeks (prior to flowering), the plants were placed under 100, 50, and 25 % of outdoor irradiance. Water was supplied as needed to keep an adequate soil moisture.

Three assimilation chambers (40×47×55 cm each) made of acrylic board (3 mm thick) were used in this experiment. The air temperature was controlled using a radiator installed inside the chamber. An air pump connected to a flow meter of capillary type was used to provide an adequate air inlet. The humidity values of inlet and outlet air were measured with two hygrometers (*Vaisala, R.H. & T Indicator HMI 14,* Uppsala, Sweden); from the difference of these values E was calculated. Sun irradiance was measured by a pyranometer sensor (*LI-200SB, Li-Cor*, Lincoln, USA), air and leaf temperatures were measured by thermocouples (copper-constantan, 1 mm ϕ). P_N was measured using an infrared gas analyzer (*ASSA-1110*, *Horiba*, Kyoto, Japan). The measuring time was 10 min for each treatment, consecutively changing the plant groups. Diffusion conductances were calculated according to the model of Gaastra (1959). All sensors used in this experiment were connected to a computer which was set for automatic measurement. The maximum irradiance outside the chamber during experiments was 1800 μmol(PAR, photosynthetically active radiation) m^{-2} s^{-1}. The ranges of air temperature inside the chambers were 24.1-35.4 (I_{100}), 23.3-33.2 (I_{50}), and 24.0-35.8 (I_{25}) °C.

After 20 d of treatments with different irradiances (46 d after sowing, flowering stage), P_N and E were measured. Since sunrise till noon they were measured under the growth irradiances, and beginning afternoon until sunset all plants were measured under 100 % irradiance. After termination of experiment, the plants were cut just above the soil level and separated into leaves and stems. The leaf area was measured using an automatic area meter (Model *AAM7*, *Hayashi Denkoh*, Tokyo, Japan), and then each plant part was dried for 5 d at 85 °C, weighed, and ground to a fine powder. The nitrogen contents of leaves and stems were measured by a nitrogen-carbon analyzer (*Sumigraph NC-80*, *Sumimoto*, Osaka, Japan).

Results

The different values of P_N among the treatments were larger when measured under growth irradiance (in the forenoon) than those measured under full irradiance in the afternoon (Fig. 2*A*). The slopes of P_N under a low irradiance during early morning or late afternoon were also slightly different: the higher the growth irradiance, the steeper was the slope.

Diurnal variation in mesophyll conductance (g_m) corresponded better to the diurnal variation of P_N than the variation in stomatal conductance to CO_2 (g_s) (Fig.

2*B*,*D*), and thus g_m was considered to have an inevitable role in photosynthesis. The lower the growth irradiance, the lower was g_m.

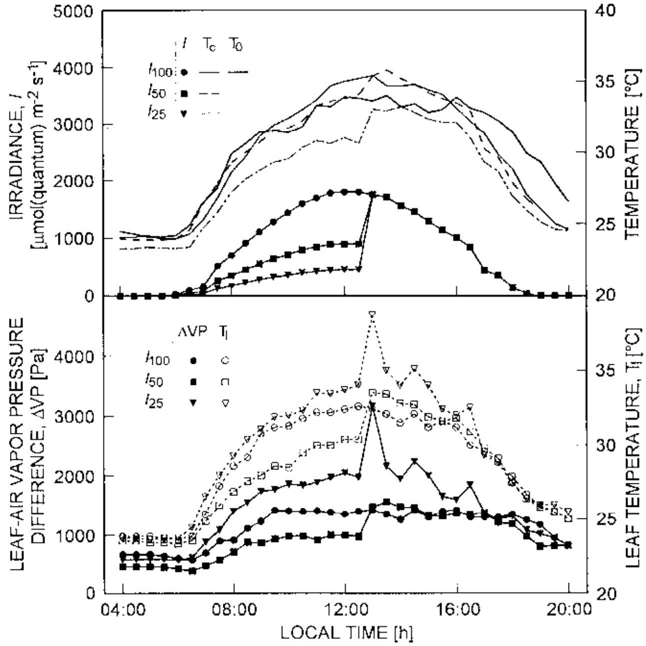

Fig. 1. Irradiance (I), air temperature outside (T_o) or inside (T_c) the chamber, leaf-air vapour pressure differences (ΔVP), and leaf temperature (T_l) during the experiment.

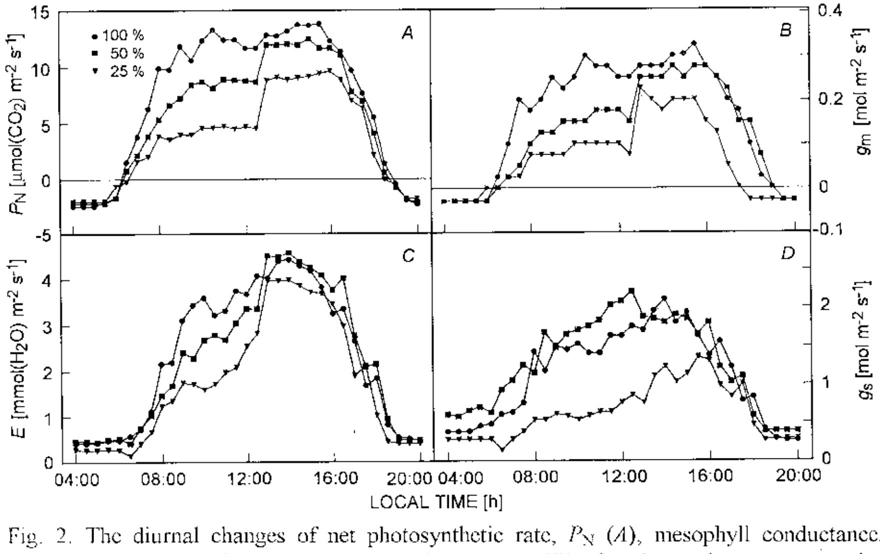

Fig. 2. The diurnal changes of net photosynthetic rate, P_N (*A*), mesophyll conductance, g_m (*B*), transpiration rate, E (*C*), and stomatal conductance, g_s (*D*) of soybean plants grown under different irradiances (I_{100}, I_{50}, I_{25} = 100, 50, and 25 % of full sun irradiance). In the morning until 12:30, plants were measured under growth irradiances, but in the afternoon, all plants were measured under full irradiance (100 %).

During morning, the higher the growth irradiance, the higher was E measured at growth irradiance. When the plants were exposed to full irradiance in the afternoon, the highest E was found in I_{50} plants (Fig. 2*C*). The g_s, responsible for variation in E, was lowest in I_{25} plants (Fig. 2*D*). In the consequence of a low E, leaf temperature (T_l) and leaf-air vapour pressure difference (ΔVP) were higher in the I_{25} plants than in plants grown under higher irradiances (Fig. 1).

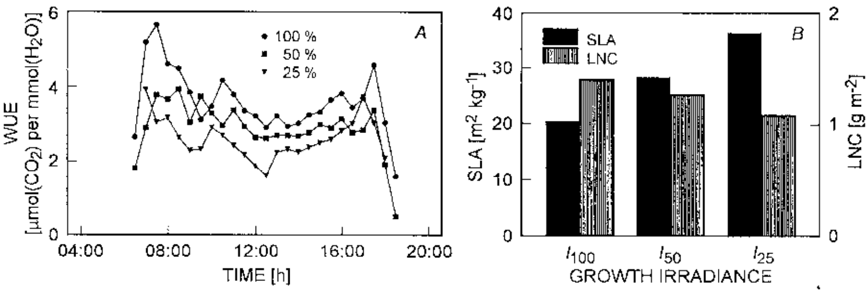

Fig. 3. The diurnal changes of water use efficiency, WUE (*A*), and specific leaf area, SLA and leaf nitrogen content, LNC (*B*) of soybean plants grown under different irradiances. For details see Fig. 2.

The water use efficiency, WUE (P_N/E ratio) was highest in I_{100} plants both during morning and afternoon measurements (Fig. 3*A*). Generally, WUE was lower at noon than after sunrise and before sunset. The leaf thickness, which was represented by specific leaf area (SLA) was highest in I_{25} plants, and the nitrogen content per leaf area in I_{100} plants (Fig. 3*B*).

Discussion

Photosynthetic characteristics were adjusted to growth irradiance (Fig. 2), similarly as in experiments with a single leaf of soybean (Bowes *et al.* 1972, Singh *et al.* 1974), in *Vicia faba* (Nikolaeva 1994), and *Plectranthus marrubioides* (Herppich 1997). The differences in P_N found at saturating irradiance among plants grown under various irradiances might refer to the differences in energy utilization due to changed leaf and chloroplast structure, and chlorophyll content (Björkman *et al.* 1972, Nikolaeva 1994). Björkman *et al.* (1972) found no significant differences among the initial slopes of P_N in *Atriplex patula* grown under different irradiances which indicated a constant quantum efficiency of photosynthesis. In our experiment, however, the differences in P_N slopes at low irradiances (Fig. 2*A*) confirmed the differences in quantum efficiency of photosynthesis.

Nobel *et al.* (1975) conclude that increased g_m of sun leaves is a consequence of the large mesophyll cell surface area per unit leaf surface. Björkman *et al.* (1972), who calculated the dependence of CO_2 uptake on stomatal resistance for *Atriplex* leaves, suggested that the resistance of stomata to CO_2 diffusion in the plants grown under different irradiances had imposed only a minor restriction on their P_N in the normal air. According to Ishii (1995), g_m in rice plays a larger role in P_N than g_s.

The I_{25} soybean plants contained less nitrogen in leaves than the I_{100} plants; this could contribute to their reduced photosynthetic activity (Evans 1989, Arima 1995). Takenaga (1995) stated that although the effect of irradiance on nutrient (including nitrogen) absorption was indirect, their absorption decreased with decreased irradiance. In the same way, the low growth irradiances are responsible for increased SLA or decreased leaf thickness; this might deteriorate leaf structure (Björkman *et al.* 1972, Lichtenthaler *et al.* 1981), change absorbance of leaves (Rabinowitch 1951, Terashima and Saeki 1985), and thus decrease their photosynthetic activity. In addition, increased T_l values were found in I_{50} and I_{25} plants. According to Wahua and Miller (1978), an increased T_l might change the translocation of assimilates.

Though the E of I_{100} and I_{50} plants did not differ significantly during afternoon, the E and g_s of I_{25} plants were considerably lower. This may be attributed mainly to the decreasing number of stomata per unit leaf area. According to Boardman (1977), the plants grown under a low irradiance have a lower stomatal frequency and hence lower g_s than the plants grown under a high irradiance. The other factor possibly contributing to the low E of I_{25} plants was the water deficit in leaves due to the decreasing water absorption. Relating to this matter, Baharsjah (1980) found that soybean plants grown under low irradiances had less root dry matter than plants grown under normal irradiance.

Since the differences in WUE among the treatments were similar during morning and during afternoon, the WUE in soybean plants depended more on growth irradiance than on actual irradiance.

The results of present experiments verified a strong dependence of soybean plants P_N on the growth irradiance. The P_N was inhibited more than E by low growth irradiances. Therefore the differences in it due to the attenuation of radiation within the canopy should be taken into account when predicting the canopy photosynthesis of soybean.

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