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Morphophysiological and yield traits of soybean varieties tolerant of intercropping with maize

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Abstract. *Permanasari I, Sulistyaningsih E, Kurniasih B, Indradewa D. 2023. Morphophysiological and yield traits of soybean varieties tolerant of intercropping with maize. Biodiversitas 24: 3872-3880.* Not all soybean varieties grow optimally when intercropped with maize. Previously, we identified seven varieties (i.e., "Demas 1", Dena 1", "Dena 2", "Derap 1", "Devon 1", "Devon 2", and "Wilis") and two (i.e., "Dega 1" and "Mahameru") as tolerant and intolerant of intercropping based on selection indices and yield. This research aims to determine the morphophysiological and yield traits of tolerant and intolerant soybean groups intercropped with maize. The study used a randomized complete block design with three blocks as replications, and conducted from October 2019 to February 2020. Results showed that light intensity in the intercropping system had decreased by 19.91% relative to that in the monoculture system at 7 weeks after planting. The tolerant group displayed significant gains in seed weight per plant (143.66%), total biomass (50.04%), harvest index (53.33%), total number of pods and seeds per plant (119.39% and 128.86%), leaf nitrogen uptake and content (20.83% and 6.44%), chlorophyll-a:b ratio (7.20%), and stem diameter (7.65%) than the intolerant group. Correlation analysis revealed that leaf nitrogen content showed the highest correlation and significantly contributed to seed weight per plant in the tolerant and intolerant groups. Seed weight in the tolerant group was mainly affected by morphological (total biomass and harvest index), physiological (leaf nitrogen content), and yield components (number of pods), whereas that in the intolerant group was influenced only by physiological parameters (nitrogen content). Nitrogen content was considered suitable as a selection indicator for determining the seed yield of intercropped soybean varieties. Furthermore, using soybean tolerant groups for intercropping may be a solution to increase soybean production in Indonesia.

Keywords: Intercropping, photosynthate, soybean, yield

INTRODUCTION

Soybean (*Glycine max* L), known as a miracle golden bean due to its nutritive value (Zinia et al. 2022), is one of Indonesia's three most important and valuable crops, along with rice and maize (Erythrina et al. 2022). Soybean production in Indonesia is decreasing due to the reduction of harvesting area by 5% year^{-1}, while productivity is increasing by only 2% year^{-1} (Harsono et al. 2022). On the other hand, soybean consumption is steadily increasing due to the growing population and high demand for food industries. The factor contributing to this reduction is land-use competition with other important commodities, such as maize and chili, which farmers prefer because of their high revenue (Harsono et al. 2022). In addition, land degradation also contributes to this loss. The application of an innovative strategy such as intercropping soybean with other major commodities to minimize land usage competition is therefore important to achieve sustainable land use (Srihartanto and Indradewa 2019; Astiko et al. 2022) and food security (Sevirasari et al. 2022).

Soybean intercropping is potentially applicable and an essential strategy for improving national soybean production in Indonesia. The farmer is important, managing 58.73% of the agriculture area (Purnawan et al. 2022). A recent survey, however, reported that soybean-intercropping systems have low application in Indonesia. Only 23.2% of household farmers used intercropping to plant soybeans (Erythrina et al. 2022). Farmers are reluctant to apply intercropping because they remain unaware and skeptical of this system.

Intercropping soybean with maize is a popular combination (Du et al. 2018; Blessing et al. 2022), as these crops have wide adaptability with high cropping system efficiency and sustainability. Combining these crops is thought to provide several benefits, including improved light-use management, as maize is a faster-growing species that uses light primarily at the top of the canopy. In contrast, soybean is a slower-growing species that uses light at the bottom of the canopy. Another benefit is that the congenial root structure of soybean has deep and straight roots, whereas maize has fibrous and shallow roots. Soybeans can synthesize and utilize atmospheric nitrogen (N_2), which is advantageous to maize (Li et al. 2016; van Vugt et al. 2018) as it lowers competition for N_2 nutrients. It also increases soil surface coverage, reducing erosion, strangulating weeds, and preventing water evaporation.

Even though soybean-maize intercropping decreases soybean seed yield, it increases the total yields (Ren et al. 2017). One reason for this yield reduction was shade stress

(Yang et al. 2018). The high habitus of maize has been suggested to reduce the amount of light obtained by soybean. However, the difference in root structure enables mutual interaction between the two crops to retain high yields. Interestingly, different soybean varieties have diverse responses. Gong et al. (2015) noted that shading tolerance is a collection of traits that normally promotes carbon acquisition under shaded conditions. Such traits include an increase in specific leaf area, a decrease in chlorophyll-a:b ratio, and the suppression of shade avoidance characteristics. Under shaded conditions, tolerant soybean varieties intercept and use more light than non-tolerant varieties. The avoidance and adaptability of different shade-tolerant soybeans are associated with phenotype, physiology (Cheng et al. 2022), and environment (Yu-shan et al. 2017).

By 2020, the Indonesia Ministry of Agriculture had released 85 commercial soybean varieties (Krisnawati and Adie 2015). Many reports have revealed different results for the yield performance of varieties intercropped with maize (Harsono et al. 2020). Permanasari et al. (2021) previously tested 16 soybean varieties and reported that based on five selection indices (i.e., average relative seed weight, stress tolerance, mean productivity, geometric mean productivity, and yield index), "Demas 1", "Dena 1", "Dena 2", "Derap 1", "Devon 1", "Devon 2", and "Wilis" are tolerant varieties, whereas "Dega 1" and "Mahameru" are varieties intolerant of intercropping with maize. In this current research, we further conducted a detailed study focusing on the responses of the morphophysiological and yield traits of the tolerant soybean group in an intercropping system.

MATERIALS AND METHODS

Materials and experimental site

Two groups of previously selected tolerant ("Demas 1", "Dena 1", "Dena 2", "Derap 1", "Devon 1", "Devon 2", and "Wilis") and intolerant ("Dega 1" and "Mahameru") soybean varieties were used in this study. A field experiment was performed at the Rural Extension Center (*Balai Penyuluhan Pertanian*) of Seyegan, Sleman, Yogyakarta, Indonesia (latitude: -07° 43 min 49.7621 s, longitude: 110° 18 min 16.4783 s) from October 2019 to February 2020. The soil was a silt loam with a pH of 6.5 and availability of nitrogen total, nitrogen, phosphorus, and potassium of 0.19%, 0.02%, 131.50 ppm, and 180.00 ppm, respectively.

Methods

The study used a randomized complete block design with three blocks as replications. The schematic of the soybean-maize planting pattern in the intercropping system in which soybean–soybean and maize–maize were arranged with interspacing of 20 and 100 cm, respectively, was depicted in Figure 1. Permanasari et al. (2021) performed agricultural practices for soybean plant maintenance. The parameters, including environmental variables (light intensity and water precipitation), physiological characters (leaf nitrogen uptake, leaf nitrogen content, chlorophyll-a, chlorophyll-b, total chlorophyll, chlorophyll-a:b ratios, stomatal density, stomatal aperture width, Leaf Area Index (LAI), light interception, Specific Leaf Weight (SLW), Net Assimilation Rate (NAR), Crop Growth Rate (CGR), total biomass, and harvest index), morphological characters (plant height and stem diameter), and yield and yield components (number of pods per plant, number of seeds per plant, and seed weight per plant) were assessed at 7 Weeks After Planting (WAP) or at harvest time.

A light meter measured the light intensity 5 cm above the soybean canopy at mid-day (~12:00) with clear skies. The light interception was subsequently calculated based on the formula of Portes and Melo (2014). Data on rainfall were obtained from the NASA climate database (https://climate.nasa.gov/) by locating the coordinates of this field trial. Chlorophyll content, chlorophyll-a, and chlorophyll-b were quantified by using the following equations from Arnon (1949):

$$Chlorophyll-content = 20.2(A_{645}) + 8.02(A_{663})$$
$$Chlorophyll-a = 12.7(A_{663}) - 2.69(A_{645})$$
$$Chlorophyll-b = 22.9(A_{645}) - 4.68(A_{663})$$

Stomatal impressions were made using nail polish and subsequently viewed under a microscope. Stomatal density and stomatal aperture width were measured by applying Optilab Viewer v2 (Miconos, Indonesia) software. Leaf area was calculated using a leaf area meter (MK2, DELTA T Devices Ltd, UK) with the assistance of WinDIAS software (DELTA T Devices Ltd, UK). Leaf nitrogen content was measured following Muarif et al. (2022), and leaf nitrogen uptake was calculated by using the formula:

$$Leaf\ nitrogen\ uptake = Leaf\ N\ content \times leaf\ dry\ weight\ per-plant.$$

SLW measurement was performed by using the following formula of Amanullah (2015):

$$SLW = Leaf\ dry\ weight\ per-plant \div Leaf\ area\ per-plant\ .$$

Leaf weight, biomass, and seed weight per plant were measured using an analytical balance (ACS AD-300i, China). The harvest index was calculated following Amanullah and Inamullah (2016).

Data analysis

All data were analyzed with standard error, and a t-test was used to determine the effect of soybean tolerance groups on morphophysiological and yield traits. The percentage of the difference between the tolerant and intolerant groups, here termed as tolerant gain (*D*), was calculated with the following formula (Su et al. 2014):

$$D = \left(\frac{Tolerant - Intolerant}{Intolerant}\right) \times 100\%.$$

Pearson correlations were calculated using StatPlus: mac (AnalystSoft Inc., USA) to determine the correlation between seed weight per plant and other variables. All data analyses were deemed statistically significant at $P < 0.05$ and marginally significant at $P < 0.10$.

RESULTS AND DISCUSSION

Environmental condition

Different light intensities at 5 cm above the soybean were observed. Morning, noon, and afternoon light intensities reached 54,791, 73,311, and 33,683 lux, respectively. Light intensities were lowest in the afternoon because of their relationship with the solar angle. In this study, the design plots for maize were positioned southwest. Therefore, the maize canopy shaded soybean plants.

Water precipitation fluctuated during soybean growth and was lowest on the first 30 Days After Planting (DAP) (52.07 mm), highest at 61-90 DAP (364.89 mm), and decreased at 91-120 DAP (247.62 mm) (https://climate.nasa.gov/). Annual crops have a water requirement of approximately 70 mm per month and thus require a precipitation level of 120 mm monthly (Fuadi et al. 2020). Therefore, water precipitation was excessive during this study.

Physiological characters

Leaf nitrogen uptake and leaf nitrogen content

Compared with the intolerant group, the tolerant group demonstrated a marginal increase in leaf nitrogen uptake (P = 0.086) and significantly higher leaf nitrogen content (P = 0.006; Table 1). Previous reports (Yong et al. 2015; Zhang et al. 2017; Fu et al. 2019) showed that nitrogen uptake by soybeans intercropped with maize was lower than soybeans in monoculture systems due to competition with maize. In this study, the intercropped tolerant group tended to have a better capacity for maintaining nitrogen uptake than the intolerant group. Nitrogen content improves leaf development because nitrogen participates in cell structure formation and development.

Chlorophyll

The findings of this work showed that the chlorophyll-a:b ratio was significantly higher in the tolerant group than in the intolerant group (P = 0.048; Table 1). However, other chlorophyll parameters, such as chlorophyll-a, chlorophyll-b, and total chlorophyll, showed non-significant differences. The habitus of soybean was shorter than that of maize, and the lack of difference in leaf size favored soybean's efficient capture of sunlight. The high chlorophyll content observed here was due to the assembly of chloroplasts at the anticlinal point of the palisade during the shading periods such that light captures efficiency increased (Liu et al. 2015). The result of this study was following the findings of Evans and Poorter (2001), Valladares and Niinemets (2008) and Gong et al. (2014). The high chlorophyll content benefits plants because chlorophyll is crucial for photosynthesis. The excitatory energy from chlorophyll promotes water reaction and subsequent electron transport separation, increasing the photosynthetic rate. The increase and decrease in chlorophyll content are associated with some enzymes that enable chlorophyll degradation (Zhang et al. 2016).

Stomatal density and stomatal aperture width

The study revealed that the tolerant and intolerant groups showed no significant differences in stomatal density (P = 0.326); they revealed a significant difference in stomatal aperture width (P = 0.034; Table 1). Stomatal density was measured on the abaxial leaf. Similar to the present study, the work of Fan et al. (2018) revealed that stomatal density on the bottom surfaces of leaves did not differ between groups.

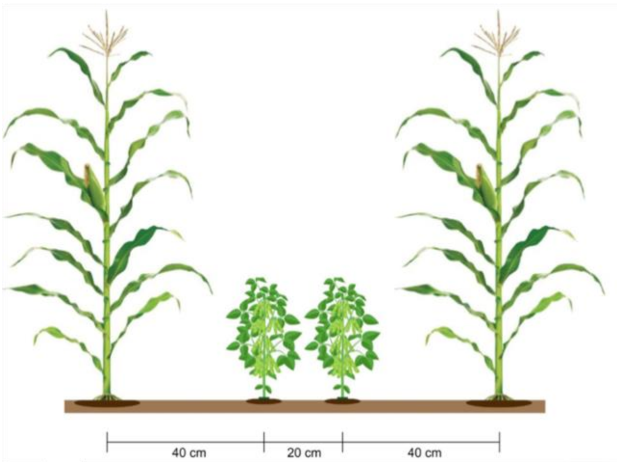

Figure 1. Schematic of the soybean–maize planting pattern in the intercropping system. Soybean–soybean, and maize–maize were arranged with interspacings of 20 and 100 cm, respectively

Table 1. Mean comparison of physiological parameters between tolerant and intolerant soybean groups and the gains of the tolerant group (D)

Physiological Parameter	Tolerant	Intolerant	Significance (P-value)	D (%)
Leaf nitrogen uptake (g of leaf dry weight^{-1})	0.29 ± 0.02	0.24 ± 0.03	0.086	20.83
Leaf nitrogen content	4.46 ± 0.05	4.19 ± 0.02	0.006	6.44
Chlorophyll-a (mg g^{-1} leaf fresh weight)	18.05 ± 2.43	17.02 ± 2.52	0.416	6.05
Chlorophyll-b (mg g^{-1} leaf fresh weight)	13.45 ± 1.77	13.62 ± 1.97	0.480	-1.25
Total chlorophyll (mg g^{-1} leaf fresh weight)	31.23 ± 4.16	30.64 ± 4.46	0.472	1.93
Chlorophyll-a:b ratio	1.34 ± 0.02	1.25 ± 0.05	0.048	7.20
Stomatal density (mm^{-2})	300.67 ± 16.67	315.50 ±15.04	0.326	-4.70
Stomatal aperture width (µm)	54.81 ± 3.79	70.90 ± 8.59	0.034	-22.69

Note: Mean ± standard error. P-value < 0.01, 0.01 < P-value < 0.05, 0.05 <P value < 0.10 indicates data was highly significant, significant, and marginally significant, respectively. P-value > 0.10 means not significant

Richardson et al. (2017) stated that plant adaptation to light intensity can be reflected by stomatal density. High light intensity causes an increase in ambient temperature, which increases the amount and density of stomata. However, Xiong and Flexas (2020) reported a negative association between the amount and density of stomata. The number of stomata decreases as the density of stomata increases due to the rapid response of small stomata to quick environmental changes. Yang et al. (2017) stated that reducing stomatal conductivity would reduce soybean productivity by disrupting CO_2 intake to optimize photosynthesis; this effect limits the diffusion of CO_2 for photosynthesis. The findings of this study clearly showed that the tolerant group had a higher seed yield than the intolerant group. Therefore, stomatal size is unsuitable as an indicator of the number of seeds produced by both varieties. The opening and closing of stomata are related to photosynthetic processes, given that stomata transport CO_2, O_2, and H_2O and absorb K^+ ions (Wasonowati et al. 2019).

Morphological characters

Leaf area index, light interception, and specific leaf weight

The LAI of the tolerant group was 15.25% higher than the intolerant group's (Table 2). This result indicated that the tolerant group possessed a higher leaf area than the intolerant group and thus had a greater capacity for capturing sunlight (Mathur et al. 2018), such that photosynthesis increased. Furthermore, this result was in line with the light interception parameter, which had increased by 6.54% in the tolerant group (Table 2). The tolerant group was assumed to have higher light interception capability than the intolerant group at intercropping. Valladares and Niinemets (2008) also mentioned that tolerant plants have larger leaf areas than intolerant, in which the increase in leaf area is affected by the lateral meristem located on the edge of the expanding young leaf (Srihartanto and Indradewa 2019). Shaded plants experience limited cell division in young leaves such that the number of cells decreases, reducing the leaf area of adult leaves (Gong et al. 2014).

The SLW of the intercropping-tolerant group was slightly reduced by 5.88% (Table 2), which was consistent with the findings of Gong et al. (2015). The tolerant group had a higher leaf area than the intolerant group due to its higher photosynthetic sources, efficiency, and capacity. However, compared with the tolerant group, the intolerant group had a higher SLW, suggesting a higher proportion of leaf weight to leaf area. Given its high leaf area and light interception, the tolerant group was expected to exhibit high dry weight. The response to shading of soybean observed in this study was consistent with that found in the study of Gommers et al. (2013), who discovered that shading-tolerant plants optimized carbon capture by increasing their leaf area. Specific leaf weight describes the thickness of leaves, and a high SLW is suggestive of thick leaves (Srihartanto and Indradewa 2019). Leaf thickness affects the density of mesophyll, palisades, and leaf sponge tissues. It is related to the cell arrangement of the leaves' mesophyll layer (Fan et al. 2018). Therefore, compared with the intolerant group, the tolerant group was more responsive to changes in light intensity and the factors necessary for growth, such as water and nutrients, from the soil, as depicted by its lower SLW.

Net Assimilation Rate (NAR) and Crop Growth Rate (CGR)

The tolerant group had a higher NAR gain (10.53%) than the intolerant group (Table 2). This result showed that the former group produced more dry materials per leaf area than the latter group. The tolerant group maintained a higher net photosynthesis rate than the intolerant group; this ability increased the average net photosynthetic rate. However, changing the canopy structure of the tolerant group was difficult (Cheng et al. 2022). Khalid et al. (2019) reported that in tolerant varieties, reducing light intensity to 25% (optimal intensity) increased the efficiency of Photosystem II (PSII) and evapotranspiration, which could increase photosynthetic capacity by increasing energy transmission from PSII to Photosystem I (PSI).

The crop growth rate of the tolerant group increased by 13.59% relative to that of the intolerant group (Table 2). Nitrogen uptake also increased NAR and CGR, thus improving crop growth rate. The high leaf area in the tolerant group allowed for increased light capture. The high leaf area also enhanced photosynthesis capacity per unit of leaf area (Su et al. 2014). This situation suggested that the tolerant group possessed better capability for producing dry material than the intolerant group during the disturbance of photosynthesis caused by the decrease in light intensity. Therefore, in the tolerant group, the accumulation of dry material produced per unit of the land area was greater under non-full-light conditions than in other conditions. Above and below-ground interactions with maize also supported this result. Su et al. (2014) reported that tolerance to shade stress was enhanced in C3 plants with a high net photosynthetic rate. Maize encouraged soybeans to increase their growth rate. Li et al. (2016) reported that maize planted alongside soybeans might release exudates that influence root deformation, nodule development, and nitrogen fixation because intercropping stimulates flavonoids and nodule secretions, as observed in faba beans. Total N_2 fixed was closely related to plant growth parameters such as grain production, biomass yield, and plant height (van Vugt et al. 2018).

Total biomass (7 WAP and harvest) and harvest index

Compared with the intolerant group, the tolerant group had higher gains in nitrogen uptake, leaf nitrogen content, stem diameter, LAI, LI, NAR, and CGR and was thus able to utilize below-ground resources for photosynthesis. Therefore, the total biomasses in this group at 7 WAP and during harvest increased by 5.46% and 50.04%, respectively (Table 2). Relative to that of the intolerant, the harvest index of tolerant group significantly increased by 53.33% ($P = 0.045$; Table 2). Harvest index of the tolerant group in this study was comparable to that of intercropped Dena 1 (0.27) (Kristiono and Muzaiyanah 2021), intercropped Wilis (0.31) and intercropped Mahameru (0.29) (Umarie and Holil 2016), and intercropped soybean with sunflower (0.3-0.32) (Nawar et al. 2020). Kakiuchi and Kobata (2006) additionally discovered that shaded soybean showed a harvest index of 0.1-0.4. This indicates that photosynthates produced in the tolerant group are largely disseminated in the seed, evidenced by increased total biomass and leaf nitrogen content. As a result, the seed weight increased. The increasing harvest index, according to Ikazaki et al. (2020), could be associated with higher whole plant nitrogen and higher nitrogen translocation efficiency. The increased of dry weight accumulation in the tolerant group compared to the intolerant group indicated that tolerant soybeans have a higher capacity for high dry matter accumulation during harvest. This difference prevents competition between maize and soybean plants in obtaining nutrients, water, and space from the soil and instead allows the two plants to support and not interfere with each other (Li et al. 2014; Yang et al. 2017a).

Plant height at 8 WAP and stem diameter at 7 WAP

Intercropping showed a significant effect (P = 0.035) on the plant height at 8 WAP, as the tolerant group was 14.46% taller than the intolerant group. This finding suggested that plants undergo adaptation and can compete with maize to obtain light for their physiological processes. Huber et al. (2021) reported that stem, leaf, hypocotyl lengthening, and apical domination are mechanisms of shading avoidance. Shading avoidance gives the plant a chance to obtain adequate sunlight to survive. It is mediated by photo-sensory receptors controlled by phytochrome A, phytochrome B, and cryptochromes associated with the R:PR ratio (Casal 2013).

The stem diameter of the tolerant group significantly increased (P = 0.038) by 7.65% relative to that of the intolerant group (Table 2). Stems with large diameters are beneficial because they can support anchorage and thus increases resistance to stem breakage (Yu-shan et al. 2017). The plants in the tolerant group had strong stems that kept them upright. The higher stem diameter in the tolerant group was consistent with the findings of Cheng et al. (2022), who found that tolerant plants have more vascular bundles, phloem, and xylem and a higher vascular ratio than intolerant plants. Furthermore, Liu et al. (2018) reported that tolerant varieties had stronger stems and higher lignin content, gene expression rates, and metabolite content under shaded conditions than intolerant varieties. Thus, these variables can be used to select varieties tolerant of intercropping.

Yield and yield components

Numbers of pods, seeds, and seed weight per plant

The tolerant group had a significantly higher number of pods than the intolerant group (P = 0.001) and presented a gain of 119.39% (Table 3). This finding suggested that the tolerant group diverted most of its photosynthates to seed formation and filling in contrast to the intolerant group. The presence of maize did not interfere with pod development and instead encouraged soybeans to distribute and assimilate to pods. This study's result agreed with the findings of Cheng et al. (2022), who found that tolerant soybeans produced more pods than intolerant soybeans. This ability is allegedly related to plants' mechanism in using available light. Plants can use light effectively and efficiently for photosynthesis despite reductions in light intensity.

Similarly, the number of seeds per plant in the tolerant group significantly improved (128.86%; P = 0.001) relative to that in the intolerant group (Table 3). This finding suggested that compared with the intolerant group, the tolerant group had more photosynthates to consume to form a higher number of seeds. The increase in the number of seeds in the tolerant group was closely related to photosynthate production (Smitchger and Weeden 2018).

In the tolerant group, seed weight per plant significantly increased by 143.66% (P = 0.005; Table 3) due to high physiological, morphological (agronomical), and yield components. High nitrogen uptake, LAI, NAR, CGR, biomass total, the number of pods, number of seeds per plant, harvest index, and low SLW increased seed weight.

The tolerant group exploited available resources such that the presence of maize did not reduce its ability to produce and distribute photosynthates to seeds. Tolerant plants avoid losses under low light intensity by regulating the spatial distribution and morphology of their canopy and the physiology of their stems. These changes were supported by the tolerant group's high relative transmission coefficient, low leaf width index, and average leaf angle. The source limitation experienced by the intolerant group reduced the delivery of photosynthates to seeds (Cheng et al. 2022).

Table 2. Mean comparison of morphological parameters between tolerant and intolerant soybean groups and the gains of the tolerant group (D)

Morphological parameter	Tolerant	Intolerant	Significance (P-value)	D (%)
LAI at 7 WAP	5.29 ± 0.33	4.59 ± 0.41	0.149	15.25
Light interception at 7 WAP (%)	69.58 ± 1.82	65.31 ± 4.93	0.613	6.54
SLW at 7 WAP (g dm−2)	0.32 ± 0.01	0.34 ± 0.03	0.191	−5.88
Net assimilation rate (g dm−2 day)	0.21 ± 0.01	0.19 ± 0.03	0.253	10.53
Crop growth rate (g m−2 day)	16.47 ± 1.29	14.50 ± 2.46	0.240	13.59
Plant height at 8 WAP	83.18 ± 2.73	72.67 ± 3.98	0.035	14.46
Stem diameter at 7 WAP	7.18 ± 0.12	6.67 ± 0.32	0.038	7.65
Total biomass (7 WAP) (g)	17.57 ± 1.04	16.66 ± 2.11	0.345	5.46
Total biomass (harvest) (g)	38.17 ± 2.13	25.44 ± 3.33	0.004	50.04
Harvest index	0.23 ± 0.02	0.15 ± 0.02	0.045	53.33

Note: WAP: Week After Planting. Mean ± standard error. P-value < 0.01, 0.01 < P-value < 0.05, 0.05 <P value < 0.10 indicates data was highly significant, significant, and marginally significant, respectively. P-value > 0.10 means not significant

Table 3. Mean comparison of yield components between tolerant and intolerant soybean groups and the gains of the tolerant group (*D*)

Yields component	Tolerant	Intolerant	Significance (*P-value*)	*D* (%)
Number of pods per plant	70.95 ± 5.63	32.34 ± 3.84	0.001	119.39
Number of seeds per plant	86.12 ± 7.38	37.63 ± 3.31	0.001	128.86
Seed weight per plant	8.65 ± 0.96	3.55 ± 0.45	0.005	143.66

Note: Mean ± standard error. P-value < 0.01, 0.01 < P-value < 0.05, 0.05 <P value < 0.10 indicates data was highly significant, significant, and marginally significant, respectively. P-value > 0.10 means not significant

As a result, the increase in seed weight in the tolerant group coincided with an increase in canopy and root dry weight. The findings of this study coincided with those of Wu et al. (2021), who found that shade-tolerant soybeans had higher seed weights than shade-intolerant soybeans. Liu et al. (2015) stated that shade-tolerant varieties with high photosynthesis efficiency can be selected to improve photosynthetic capacity and outcomes in intercropping.

Correlation analysis

In the tolerant group, nitrogen content was positively and significantly correlated with total biomass harvest (r = 0.59**), harvest index (r = 0.79**), total number of pods (r = 0.55*), and seed weight per plant (r = 0.99**, Table 4). This finding was consistent with the results of Evans and Poorter (2001). Nitrogen is an essential macro-nutrient that is needed for plant growth. Nitrogen content had the highest correlation with seed weight. The increase in total chlorophyll and stomatal opening width mediated this correlation. By contrast, nitrogen content was negatively and non-significantly correlated with NAR, LAI, crop growth rate, and total biomass at 7 WAP.

Accordingly, seed weight presented a positive and significant correlation with total biomass harvest (r = 0.57**), harvest index (r = 0.80**), and the number of pods (r = 0.55*). Therefore, we assumed that seed weight would increase as these variables increased. An increase in seed weight in this tolerant group was in line with an increase in pod and seed numbers (Table 3). A similar result was reported by Liu et al. (2017), in which the higher seed production was primarily due to an increase in the number of seeds produced by intercropped soybean plants. Therefore, this variable can be used as a marker indicator.

The number of pods also significantly correlated with the total biomass harvest (r = 0.76**). Although total biomass significantly correlated with nitrogen content at 7 WAP, the dry weight at 7 WAP lacked a tangible correlation with nitrogen content. Nitrogen content also had no significant correlation with yield components and yield against dry weight at 7 WAP. This result could be ascribed to the dramatic changes between 7 WAP and the harvesting time: During this period, the high rainfall intensity exceeded the need for soybeans, so vegetative growth continued even though the soybean plants had entered the seed filling and seed maturation phases. Nitrogen content showed a higher but non-significant correlation with other variables (i.e., nitrogen content, total chlorophyll, stomatal density, stomatal aperture width, net assimilation rate, LAI at 7 WAP, crop growth rate, and total biomass at 7 WAP).

Total biomass also showed a positive and significant correlation with stomatal density (r = 0.63**), LAI at 7 WAP (r = 0.70**), and crop growth rate (r = 0.73**). High LAI was therefore assumed to be due to the increased capture of sunlight such that photosynthesis improved (Srihartanto and Indradewa 2019) as reflected by the significant correlation of LAI with crop growth rate (r = 0.67**) and total chlorophyll content (r = 0.61**). The increase in crop growth rate was also succeeded by the increase in NAR produced (r = 0.71*) as also following Faozi et al. (2021).

In the intolerant group, nitrogen content showed a significant and positive correlation (r = 0.97**) only with seed weight (Table 5). Meanwhile, seed weight was not significantly correlated with other variables. Furthermore, the pod number significantly correlated with total chlorophyll (r = 0.87*). This relationship indicated that the number of pods would increase with the total chlorophyll increase but decrease with stomatal aperture width (r = -0.81*). The produced pods in this group dominantly developed on branches. Wide stomatal opening increases CO_2 entry into leaves. Still, it cannot compensate for the photosynthetic ability of leaves, thus reducing the number of pods and total biomass (r = -0.84*). Total biomass would increase with NAR (r = 0.83*) and crop growth rate (r = 0.98**). NAR and CGR were significantly correlated (r = 0.89*). Furthermore, NAR was correlated with stomatal density (r = 0.90*) and increased with the increase in stomata density due to the increase in LAI (r = 0.85*).

In both soybean groups, seed weight increased as nitrogen content increased, which was consistent with Ciampitti and Salvagiotti (2018), who further revealed that it was also correlated with N fixation. The amount of photosynthate needed for growth supplied to all plant organs possibly increased, given that high nitrogen content levels improved plants' growth and development. In intercropping, high nitrogen absorption increased the formation of total biomass because plant metabolic processes were enhanced. Leaf nitrogen content is suspected to correlate with cytokinin and abscisic acid hormonal metabolism (Luo et al. 2018). Nitrogen is the main contributor to amino acid and protein synthesis (Perchlik and Tegeder 2018) and is an influential nutrient in plant growth (Rahayu et al. 2019). Plants could not exploit all of the nitrogen available in nature. Plants' NO^{3-} and NH^{4+} absorption allows them to form numerous nitrogenous compounds (Tho et al. 2017). Soybean requires high nitrogen levels and absorbs 55.4 kg of nitrogen per ton of grain produced (Yang et al. 2017b).

Table 4. Pearson correlations among the physiological and morphological characters, yield components, and yield of the intercropping-tolerant soybean group

	X1	X2	X3	X4	X5	X6	X7	X8	X9	X10	X11	X12
X1	1											
X2	0.14	1										
X3	−0.02	0.26	1									
X4	0.05	−0.24	0.33	1								
X5	−0.13	−0.07	0.14	−0.25	1							
X6	−0.08	0.61**	0.44	−0.11	0.18	1						
X7	−0.20	0.15	0.39	−0.09	0.71*	0.67**	1					
X8	−0.28	0.32	0.63**	−0.05	0.35	0.70**	0.73**	1				
X9	0.59**	0.04	−0.02	0.07	−0.11	0.06	−0.23	−0.39	1			
X10	0.79**	0.10	0.05	0.00	−0.09	−0.16	−0.11	−0.01	0.01	1		
X11	0.55*	−0.01	0.21	0.42	−0.29	0.24	−0.04	−0.10	0.76**	0.17	1	
X12	0.99**	0.11	−0.01	0.05	−0.11	−0.09	−0.18	−0.27	0.57**	0.80**	0.55*	1

Note: X1: Nitrogen Content, X2: Total Chlorophyll, X3: Stomatal Density, X4: Stomatal Aperture Width, X5: Net Assimilation Rate, X6: LAI 7 WAP, X7: Crop Growth Rate, X8: Total Biomass at 7 WAP, X9: Total Biomass Harvest, X10: Harvest Index, X11: Number of Pods, X12: Seed Weight Per Plant. ** and * indicate statistically significant correlations at $P < 0.01$ and $P < 0.05$, respectively

Table 5. Pearson correlations among the physiological and morphological characters, yield components, and yield of the intercropping-intolerant soybean group

	X1	X2	X3	X4	X5	X6	X7	X8	X9	X10	X11	X12
X1	1											
X2	−0.52	1										
X3	−0.70	0.74	1									
X4	0.44	−0.80	−0.47	1								
X5	−0.51	0.43	0.90*	−0.20	1							
X6	−0.37	0.77	0.85*	−0.29	0.73	1						
X7	−0.42	0.08	0.72	0.19	0.89*	0.54	1					
X8	−0.34	0.05	0.67	0.19	0.83*	0.47	0.98**	1				
X9	−0.08	0.68	0.07	−0.84*	−0.23	0.15	−0.62	−0.63	1			
X10	0.75	−0.67	−0.42	0.69	−0.13	−0.29	0.17	0.29	−0.63	1		
X11	−0.26	0.87*	0.33	−0.81*	−0.03	0.46	−0.41	−0.46	0.93**	−0.72	1	
X12	0.97**	−0.31	−0.56	0.25	−0.44	−0.22	−0.42	−0.32	0.08	0.69	−0.08	1

Note: X1: Nitrogen Content, X2: Total Chlorophyll, X3: Stomatal Density, X4: Stomatal Aperture Width, X5: Net Assimilation Rate, X6: LAI 7 WAP, X7: Crop Growth Rate, X8: Total Biomass at 7 WAP, X9: Total Biomass Harvest, X10: Harvest Index, X11: Number of Pods, X12: Seed Weight Per Plant. ** and * indicate statistically significant correlations at $P < 0.01$ and $P < 0.05$, respectively

Iqbal et al. (2019) mentioned that the interaction between soybean-maize increases N uptake and prevents N loss, thus increasing biomass. Leaf nitrogen content could be used to select soybeans that potentially yield the maximum. Yu-shan et al. (2017) discovered a positive and highly-significant correlation ($r = 0.47^{**}$) between vegetative development period and the weight of soybean seeds in soybean intercropped with maize. Kasu-Bandi et al. (2019) reported that seed yield of soybean had significantly correlation ($r=0.42^{**}$) with fresh biomass.

In conclusion, tolerant and intolerant soybean varieties showed different morphological, physiological, yield components, and yield parameters responses at intercropped cultivations. Compared with the intolerant group, the tolerant soybean group showed significantly greater (143.66%) gains in seed weight per plant. Even though the tolerant group did not show considerable increases in chlorophyll content, total stomata, NAR, and LAI with the increase in nitrogen content, they still presented a high total biomass harvest, number of pods, and seed weight. In addition, the leaf nitrogen content exerted a significant major influence on seed weight in intercropping-tolerant soybeans. As a result, this soybean group is applicable for intercropping with maize to support Indonesian government programs aiming to achieve self-sufficient soybean production and thus reduce imports.

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