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Optimizing the growth and production of sorghum by intercropping with peanuts under effective photoprotection

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ABSTRACT

This peanut-sorghum intercropping study examined the effects of peanut habit of posture (one erect and one semi-erect accession) on dwarf sorghum growth and yield over two years under field conditions. In northern China, the dwarf sorghum (*Sorghum bicolor* [L.] Moench) is an important and widely planted industrial crop for ethanol fermentation. Substantial efforts are in progress to reduce the negative environmental impacts arising from sorghum monocultures and other conventional farming practices. Intercropping, especially with nitrogen-fixing legumes, was identified as one of the effective and sustainable agricultural practices for maintaining productivity while minimizing ecological impacts. In this study, the intercropping of a dwarf sorghum cultivar with peanuts (two accessions) increased the sorghum yield over two crop cycles. Relative to peanuts planted in monocultures, the intercropping process with sorghum generally reduced peanuts' yield. Specifically, intercropping lowered the total dry matter, yield, and leaf net photosynthetic rates (Pn) in both peanut accessions. Conversely, in the semi-erect peanut-sorghum system, the total seed yield of the peanut-sorghum system increased by 19.5% in 2021 and 21.2% in 2022, resulting in a land equivalent ratio (LER > 1), whereas the erect peanut-sorghum system failed to deliver better outcomes (LER < 1). Interestingly, the semi-erect habit mitigated intercropping-induced yield losses in peanuts while conferring a significant yield advantage to sorghum compared to the erect system. From the photosynthesis perspective, the intercropped peanut plants had lower quantum yields of photosystems I (PSI) and II (PSII) than the monocultured peanuts; and this inhibition was less pronounced in the semi-erect peanuts. Additionally, the cyclic electron flow (CEF), proton gradient (ΔpH), and non-photochemical quenching were higher in intercropped peanuts than in monocultured peanuts. The increased foliar CEF and ΔpH plausibly helped the semi-erect type peanut to alleviate photoinhibition and growth reduction in the peanut-sorghum intercropping system. These enhanced photoprotective mechanisms (increased CEF and ΔpH) facilitated photosynthetic acclimation in the semi-erect peanuts, highlighting the value of habit-specific selection for optimizing sorghum-peanut intercropping.

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1. Introduction

The glutinous sorghum (*Sorghum bicolor* (L.) Moench) is widely used globally for the production of sugar, feed, paper, and ethanol fermentation (Bai et al., 2017; Li et al., 2024). Global food, feed, and bioenergy demand continue to rise (Binns et al., 2021; Yang et al., 2022), especially ethanol production in the context of food security, which is an urgent issue to be addressed. Moreover, intensive farming practices often degrade soil quality, overuse water and nitrogen resources, and contribute to environmental pollution (Erisman et al., 2008; Gianfreda et al., 2005; Tyagi et al., 2022). Effective and sustainable agricultural practices are thus essential to maintaining productivity while minimizing ecological impact (Abbott et al., 2018; Mazurenko et al., 2025; Musa et al., 2012; Raseduzzaman and Jensen, 2017; Sani et al., 2025).

Intercropping refers to the practice of growing multiple crops simultaneously on the same plot of land with overlapping growth periods (Mead and Willey, 1980; Ruillé et al., 2026). Sorghum intercropping (with legumes showing the highest nitrogen fertilizer equivalent ratio) can make full use of light and heat resources and increase the production output value per unit of land (Bo et al., 2025). As a widely adopted strategy globally, it provides several sustainable advantages, including higher yields, reducing the occurrence of pests and diseases, and improving weed control (Liebman and Dyck, 1993; Raseduzzaman and Jensen, 2017; Gu et al., 2021). Intercropping can also preserve or improve soil quality (Li et al., 2021; Dowling et al., 2023), enhance biodiversity (Bourke et al., 2021; Ma et al., 2022), reduce fertilizer and water requirements (Cong et al., 2015; Tilman, 2020; Bourke et al., 2021; Mazurenko et al., 2025), lower pest and disease incidence (Gaba et al., 2015), and increase farm profitability (Tilman, 2020; Ünay et al., 2021), aligning with sustainable development goals. The use of intercropping systems to optimize the production of dwarf sorghum may be an effective strategy that takes into account ethanol production, food security, and environmental safety (Bo et al., 2025).

During the Green Revolution of the 1960s, breeding efforts to increase grain yields led to the development of dwarf varieties with improved lodging resistance. However, sustaining high yields of dwarf sorghum requires substantial fertilizer inputs, the overuse of which can lead to environmental pollution (Abbott et al., 2018; Elumalai et al., 2025; Jwaideh et al., 2022; Wu et al., 2020b). Reducing fertilizer input for dwarf cereals is essential for environmentally sustainable agriculture. Cereal-legume intercropping is a common practice that leverages the resource-complementary nature of the two crops (Brooker et al., 2015; Bo et al., 2025). By fixing nitrogen, legumes contribute to crop complementarity (Jensen et al., 2020; Demie et al., 2022; Mazurenko et al., 2025), potentially making legume–dwarf cereal combinations, such as peanut-sorghum intercropping, highly sustainable. Peanut (*Arachis hypogaea* L.), a valuable industrial oil and high-protein crop (Shi et al., 2020, 2025), has become increasingly important in China as a replacement for soybean imports and a means of enhancing food security (He et al., 2019; Sun et al., 2022; Wu et al., 2025). Both peanut and sorghum are widely cultivated in northern China. However, the continuous monocropping of peanut or sorghum increases the risk of soil-borne diseases, such as peanut stem rot and bacterial wilt, as well as sorghum head smut disease, etc. (Bai et al., 2017; Chen et al., 2020; Fan et al., 2020; Deng et al., 2024; Prom et al., 2024; Ren et al., 2024). Cereal-legume intercropping, as a common intercropping system, enables significant reduction of diseases and efficient and complementary utilization of resources (Raseduzzaman and Jensen, 2017). Contradictory results have been reported in different studies on the intercropping system of sorghum and cowpea, with sorghum showing yield increases (Musa et al., 2012; Egesa et al., 2016) and decreases (Karanja et al., 2014; Moi et al., 2021). These discrepancies may be attributed to differences in environmental conditions and crop cultivars (Moi et al., 2021). Therefore, selecting locally adapted crops and varieties is crucial for maximizing the yield potential of intercropping systems. Given its nitrogen-fixing ability (Chuong and Tri, 2024; Jiang et al., 2022) and economic importance as an oil crop (Variath and Janila, 2017; Song et al., 2022), peanut is a good selection for intercropping with sorghum. Moving forward, optimizing sorghum production by partnering with peanuts in northern China through a peanut-sorghum intercropping system can be an effective strategy (Shi et al., 2021, 2023; Bo et al., 2025).

The land equivalent ratio (LER) is a common index to assess intercropping efficiency (William, 1979; Mead and Willey, 1980). It reflects differences in land utilization efficiency by comparing yields between intercropping and monocropping, where an LER greater than 1 means that the system produces a greater yield per unit area than monocultures (Wu et al., 2016). However, intercropping efficiency usually depends on the component species or even the cultivars participating in the mixtures (Ajal et al., 2021). For example, about 85% of legume–grain intercropping systems achieve an LER above 1, while 15% do not, underscoring the need for careful cultivar selection (Demie et al., 2022).

Crops positioned lower in the canopy of intercropping systems often encounter shading and fluctuating light throughout the day, diminishing their photosynthetic carbon gains. This shading effect can reduce net photosynthesis and photochemical efficiency in crops such as soybean and peanut (Yao et al., 2017; Han et al., 2022; Dang et al., 2023). For example, soybean (*Glycine max* (L.) Merr.) positioned beneath taller maize (*Zea mays* L.) encounters reduced light in the early morning and later afternoon (Yao et al., 2017). A key photoprotective response under such unfavourable conditions involves the down-regulation of foliar PSII activity, leading to decreased quantum yield, electron transport, and photochemical quenching (Kono and Terashima, 2014; Sun et al., 2022). Generally, the non-photochemical quenching (NPQ) plays a critical role in this process by down-regulating photosynthetic electron transport as a photoprotective response (Giacometti and Morosinotto, 2013; Kono and Terashima, 2014; Wu et al., 2020a). In mung bean (*Vigna radiata* (L.) R. Wilczek), the actual PSII quantum yield [Y(II)] decreased with increased shading, with NPQ initially increasing under low shading but subsequently decreasing at higher levels (Dang et al., 2023). The peanut–maize intercropping systems showed variable results regarding the photosynthetic responses of peanut plants. For example, while the net photosynthesis rate (Pn) in peanut decreased during intercropping, the Y (II) and photochemical fluorescence quenching (qP) increased, and non-photochemical fluorescence quenching (qN) decreased (Han et al., 2022). Despite this reduction in Pn, another study similarly reported that the maximum quantum yield of PSII (F_v/F_m) in intercropped peanut plants had been enhanced (Jiang et al., 2022). In soybean-maize intercropping system, soybean experienced morning and late afternoon shading, it received light levels similar to monoculture during midday causing significant foliar photoinhibition (Yao et al., 2017). These findings highlighted that intercropping effects on foliar photosystem activity could be highly variable, depending on the specific crop arrangement, stature (or habit) and environmental conditions, which can result in either reduced or enhanced photosynthetic efficiency.

Crops with low stature in intercropping systems are more vulnerable to light fluctuation during early growth stages (Yao et al., 2017). Photoprotective responses to these fluctuations vary among crops and cultivars (Feng et al., 2021b). The cyclic electron flow (CEF) is an essential photoprotection mechanism that maintains foliar photosystem activity when encountering unfavourable conditions by facilitating continuous electron flow and balancing NADPH and ATP production (Allakhverdiev et al., 2005; Storti et al., 2020; Ma et al., 2021a). Moreover, CEF contributes to proton accumulation in the thylakoid lumen which maintains the proton gradient (ΔpH) (Storti et al., 2020; Sun et al., 2022) essential for protecting PSI and PSII from damage under fluctuating light (Huang et al., 2019). The high ΔpH-induced NPQ can prevent PSII damage (Barbato et al., 2020; Ma et al., 2021a), while reduced cytochrome ($Cytb_6f$) complex activity under high ΔpH protects PSI from excessive electrons (Yamamoto and Shikanai, 2018; Huang et al., 2019; Storti et al., 2020; Sun et al., 2024). Thus, the photoprotection mechanisms are likely to play a critical role in facilitating the acclimation of low-stature crops in intercropped systems. However, limited studies have specifically investigated these mechanisms in peanut plants within the peanut-sorghum intercropping systems.

The peanut-sorghum intercropping practice is common for the farmers in Liaoning, northern China (Shi et al., 2021, 2023; Bo et al., 2025). In terms of developmental biology, the peanut is an unusual legume plant where the flowers are produced aboveground, but the fruits develop underground (Pittman, 1995). With an indeterminate growth pattern, the peanut plant is comprised of an erect main shoot and several lateral shoots (branches) that begin at the base of the plant. The genetic control and inheritance of branching habit in peanuts have been studied extensively (Kayam et al., 2017; He et al., 2024). Thus, the development pattern and branching habit of peanuts would have a major impact on physiology (especially light interception, dynamic light perturbations, photosynthesis), productivity, and crop management (for example, distance between the flowering buds and the ground) in monoculture and intercropping scenarios. With these multi-faceted considerations, the productivity of such cultivation systems relies on the specific peanut cultivar chosen (Ajal et al., 2021); yet little is known about how various peanut accessions (or varieties), with different habits, respond to light interception and utilization under intercropping conditions with other species. The tolerance of peanuts to unfavourable conditions such as shading, excessive light (especially leading to photoinhibition), and others, is crucial to achieving high yield in intercropped systems. Thus, this intercropping study examines the effects of peanut habit (two accessions or varieties) on dwarf sorghum growth and yield over two years under field conditions. Specifically, it focused on (i) examining the biomass and yield differences between peanut accessions in intercropped and monoculture systems; (ii) assessing the effects of intercropping on peanut physiology (gas exchange, PSI and PSII activity, NPQ, CEF, and ΔpH) for the two accessions with different habit; and (iii) determining the plausible photoprotection mechanisms in intercropped peanuts within the peanut-sorghum intercropping framework.

2. Materials and methods

2.1. Plant material and experimental design

This study was conducted over two years in the experimental center of the Liaoning Academy of Agricultural Sciences (41°49’ N, 123°33’ E, 51 m a.s.l.) from May to September in 2021 and 2022. In northern China, Shenyang’s temperate continental climate experiences an average annual rainfall of 665 mm (2021–2022; heavier rains from June to September. Two peanut accessions, IGC721 (semi-erect type) and IGC4670 (erect type), were provided by the International Crops Research Institute for the Semi-Arid Tropics (ICRISAT). These accessions were selected based on differences in plant stature, branching pattern, and branch number, with similar mature plant heights. Additional accession details, including Digital Object Identifier, origin country, and genomic data, are available from ICRISAT (Upadhyaya et al., 2014). Additionally, the semi-erect habit of our peanut accession IGC721 is morphologically similar to the “bunch” phenotype descriptors by Pittman (1995). The dwarf sorghum cultivar “Liaonuo 10”, which is a dwarf glutinous sorghum cultivar grown for ethanol fermentation and widely cultivated in Liaoning Province, was also used in the experiment.

Peanut and sorghum were sown on 12 May and harvested on 3 Oct 2021; in the following year, the two crops were sown on 15 May and harvested on 1 Oct 2022. The soil characteristics (brown soil) before planting were as follows: 16.2 g kg^{-1} organic C, 108 mg kg^{-1} alkaline hydrolyzable nitrogen, 68 mg kg^{-1} available K, 29.7 mg kg^{-1} P-Olsen, 0.98 mg g^{-1} total P, and pH 6.7.

Five treatments were used: erect-type peanut monoculture (H), semi-erect type peanut monoculture (L), sorghum–erect type peanut intercropping (S+H), sorghum–semi-erect type peanut intercropping (S+L), and sorghum monoculture (S, for yield and biomass analysis only). The treatment plots (4.0 m long × 1.5 m wide) were arranged in a randomized design with three replicates (15 plots total) (Fig. 1). The distance between adjacent plots was 1 m. The intercropping plots contained four rows of peanut (nine plants per row, 4.67 plants m^{-2}) in the center two rows of sorghum (seven plants per row, 6.0 plants m^{-2}) on each side (Fig. 1a); monoculture plots contained eight rows of sorghum (seven plants per row, 9.33 plants m^{-2}) (Fig. 1b) or eight rows of peanut (nine plants per row, 12.0 plants m^{-2}) (Fig. 1c). Row spacing was 0.5 m, with plant spacing at 0.15 m for peanut and 0.2 m for sorghum. There were nine peanut plants per row, while sorghum had seven (Fig. 1). All plots received 740 kg ha^{-1} of NPK (17−17−17) fertilizer, incorporated into the soil at a depth of 0.2 m. Groundwater irrigation was provided twice weekly to deliver sufficient watering to all plants. Agronomic practices followed local guidelines for sorghum and peanut cultivation, including pest and disease management.

2.2. Plant sampling and measurements

Plant height and stem diameter were measured with a ruler and vernier caliper at 50, 60, and 70 days after planting. Gas exchange parameters [net photosynthetic rate (Pn), stomatal conductance (g_s), transpiration rate (Tr), and intercellular CO$_2$ concentration (C_i)] were recorded on the same leaf used for chlorophyll and flavonoid measurements using an open system (GFS-3000, Heinz Walz GmbH, Effeltrich, Germany) at 50, 60, and 70 days after planting (Shi et al., 2020). Measurements were taken under a photosynthetic photon flux density of 1000 μmol photons m^{-2} s^{-1}, air flow rate of 750 μmol s^{-1}, CO$_2$ concentration of 420 μmol CO$_2$ mol^{-1}, 60% relative humidity, and 25℃ leaf temperature.

Chlorophyll fluorescence and P700 parameters were measured on the third-youngest fully-expanded peanut leaf using the Dual-PAM 100 (Heinz Walz, Effeltrich, Germany), following the method described elsewhere (Shi et al., 2020; Song et al., 2020; Wu et al., 2020a). Cyclic electron flow was calculated as CEF = ETR(I) – ETR(II) (Wu et al., 2020a; Song et al., 2022). The proton gradient (ΔpH) was analyzed from P515 signal changes after 12 h of full dark adjustment (Song et al., 2020; Wu et al., 2020a; Sun et al., 2023). Actinic light (AL,630 μmol quanta m^{-2} s^{-1}) was turned on at the start and off at 220 s (Supplementary Fig.1). After analyzing P515 signal light-off responses, ΔpH was assessed accordingly.

Peanut and sorghum plants were harvested at maturity. The above- and belowground plant parts were separated, with the roots washed, oven-dried at 105℃ for 0.5 h, then 70 h at 65℃, and weighed. Peanut pods and sorghum grains were air-dried and weighed. Leaf chlorophyll and flavonoid indices were determined at 50, 60, and 70 days after planting using the Multiplex Research system (Force-A, Paris, France). The intercropping advantage was assessed using the relative yield total (RYt), calculated as:

$$RYt = B_{IS}/B_S + B_{IP}/B_P$$

where B_{IS} and B_S are the biomass (shoot + root dry weights) of intercropped and monocropped sorghum, respectively, and B_{IP} and B_P are the biomass (shoot + root dry weights) of intercropped and monocropped peanut, respectively. An RYt > 1.0 indicates an intercropping advantage, while an RYt < 1.0 indicates an intercropping disadvantage (Willey and Rao, 1980).

The land equivalent ratio (LER) and peanut-specific LER (LERp) were calculated as:

$$LER = PIS/PS + PIP/PP$$

$$LERp = PIP/PP$$

where P_{IS} and P_S are the yields of intercropped and monocropped sorghum, respectively, and P_{IP} and P_P are yields of intercropped and monocropped peanut, respectively. An LER > 1 (or < 1) indicates land use efficiency gains (or losses) with intercropping. The yield increase of

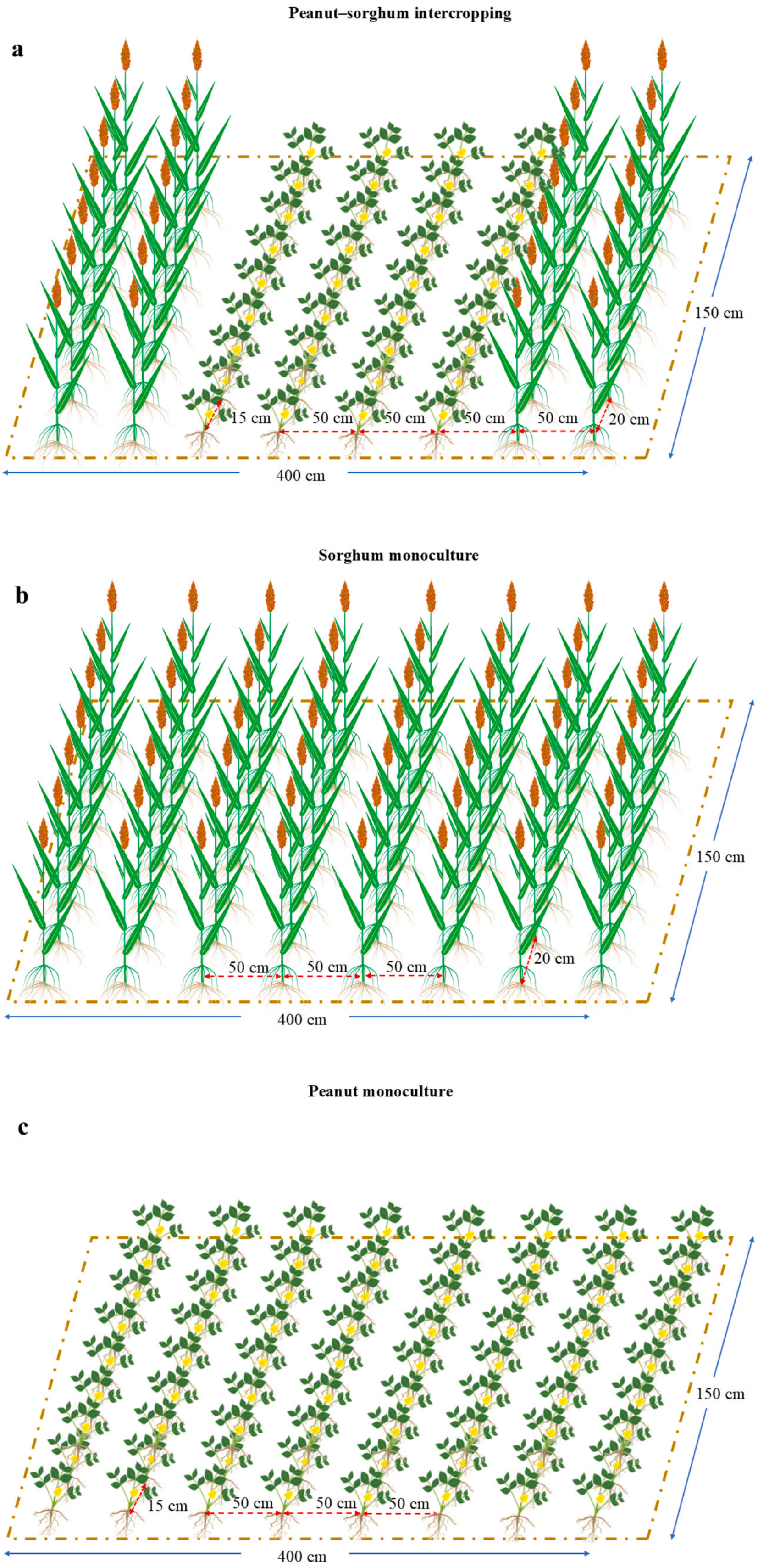

Fig. 1. Field plot layouts for planting systems (a) peanut-sorghum intercropping plot, with four rows of peanut (nine plants per row) in the center two rows of sorghum (seven plants per row) on each side. Monoculture plots with (b) eight rows of sorghum (seven plants per row) or (c) eight rows of peanuts (nine plants per row).

intercropping is calculated as (LER-1)× 100% is the yield increase of intercropping (Mead and Willey, 1980).

The aggressivity of sorghum relative to peanut (ASRP) was defined as:

$$ASRP = B_{IS}/(B_S A_S) - B_{IP}/(B_P A_P)$$

where A_S and A_P are the proportion of sorghum and peanut in the intercropping system (Willey and Rao, 1980); both were set at 50%. An ASRP > 0 indicates greater sorghum competitiveness, while ASRP < 0 indicates greater peanut competitiveness.

2.3. Statistical analyses

Data visualizations, including column, line, and violin plots were created in GraphPad Prism 9.5. Statistical analyses were conducted using one-way ANOVA in Origin 2023. The results are presented as means and standard errors for three biological replicates. Differences among treatments were identified using Fisher's LSD tests at $P = 0.05$ with non-shared letters indicating significant differences among treatments.

3. Results

3.1. Biomass, relative yield total, and the relative aggressivity of intercropping crops

The RYt for the S+L intercropping system was greater than 1 in 2021 and 2022 (Fig. 2a, b) but remained below 1 for the S+H treatment in both years (Fig. 2a, b). The S+L intercropping system significantly increased total LER (Fig. 2c, d) but reduced peanut yield (Fig. 2g, h). In 2021 and 2022, the S+L treatment had an LER greater than 1, corresponding to yield increases of 20% and 21%, respectively. In contrast, the S+H treatment had an LER near 1 in both years, with a slight yield reduction of 1% in 2021 and no effect in 2022 (Fig. 2e, f). Sorghum exhibited significantly higher aggressiveness toward the semi-erect L-type peanut than toward the erect H-type peanut (Fig. 2i, j).

Effects of intercropping on the land equivalent ratio of sorghum (LERs) in (a) 2021 and (b) 2022. Values are means ± SE ($n = 3$). Different letters indicate significant differences between sorghum/semi-erect type peanut intercropping (S+L) and sorghum/erect type peanut intercropping (S+H) at $P < 0.05$.

3.2. Plant growth

The S+L and S+H treatments produced taller peanut plants than the monocultures (Fig. 3a, b). Both intercropping treatments decreased peanut stem diameter compared with monocultures (Fig. 3c, d) but increased leaf chlorophyll concentration (Fig. 3g, h). Moreover, both intercropping treatments increased the flavonoid index of peanut leaves compared with their respective monocultures (Fig. 3e, f).

The S+L and S+H treatments also produced taller sorghum plants than the monocultures (Supplementary Fig. 3a, b). Both intercropping treatments increased sorghum stem diameter compared with monocultures (Supplementary Fig. 3c, d). Moreover, both intercropping treatments increased the flavonoid index (Supplementary Fig. 3e, f) and leaf chlorophyll concentration (Supplementary Fig. 3 g, h) of sorghum leaves compared with their respective monocultures.

Effects of intercropping on sorghum (a, b) plant height, (c, d) stem diameter, (e, f) flavonoid index, and (g, h) chlorophyll index at 50, 60, and 70 days after planting in 2021 and 2022. Values are means ± SE ($n = 3$). Different letters indicate significant differences among treatments at $P < 0.05$. Treatments are as follows: L = semi-erect type peanut monocropping, S+L = sorghum/semi-erect type peanut intercropping, H = erect type peanut monocropping, and S+H = sorghum/erect type peanut intercropping, respectively.

3.3. Leaf gas exchange

Compared with monocultures, intercropping significantly reduced Pn and g_s (Fig. 4a–d) and increased C_i (Fig. 4e, f) of peanut leaves at 50, 60, and 70 days after planting. The S+H treatment resulted in a lower Tr than the H treatment (Fig. 4g, h).

3.4. Photosystem activity

Compared with the H treatment, the S+H treatment produced a 4 −6% lower peanut Y(I) in 2021; and 6 −8% lower in 2022 (Fig. 5a, b); an 8 −11% lower peanut Y(II) in 2021; and 12 −14% lower in 2022 (Fig. 5c, d) at 50, 60 and 70 days after planting. Compared with the L treatment, the S+L treatment had a 0–2% lower peanut Y(I) in 2021; and 2 −4% lower in 2022 (Fig. 5a, b); a 6 −11% lower peanut Y(II) in 2021 and 9 −10% lower in 2022 (Fig. 5c, d). Compared with the H treatment, the S+H treatment resulted in a decrease in F_v/F_m; the S+L treatment only slightly decreased F_v/F_m compared with the L treatment (Fig. 5e, f).

Treatments are as follows: L = semi-erect type peanut monocropping, S+L = sorghum/semi-erect type peanut intercropping, H = erect type peanut monocropping, and S+H = sorghum/erect type peanut intercropping.

3.5. ΔpH

The S+L treatment increased the ΔpH of peanuts by 4 −22% in 2021; and 6 −26% in 2022 at 50, 60, and 70 days after planting, compared with the L treatment (Fig. 6a, b) and the S+H treatment increased ΔpH by 14 −22% in 2021; and 21 −28% in compared with the H treatment (Fig. 6a, b).

3.6. NPQ and CEF

The S+L treatment increased NPQ by 49%, 29%, and 16% in 2021; and 50%, 30%, and 16% in 2022 at 50, 60, and 70 days after planting, respectively, compared with the L treatment (Fig. 7a, b). The S+H treatment increased NPQ values by 23%, 21%, and 19% in 2021; and 22%, 20%; and 24% in 2022 at 50, 60, and 70 days after planting, respectively, compared with the H treatment (Fig. 7a, b). The S+L and S+H treatments had significantly higher peanut CEF values than the L and H treatments, which was more pronounced in the L treatment (Fig. 7c, d).

4. Discussion

4.1. Effect of different peanut/dwarf sorghum intercropping systems on plant growth and development

Specifically, the semi-erect peanut–dwarf sorghum intercropping system achieved an LER exceeding 1, resulting in a yield increase of ~20% for both years. Conversely, the erect peanut–dwarf sorghum intercropping system exhibited an LER near or below (Fig. 2c–f). Previous research had reported that the LERs were greater than 1 in various peanut-sorghum combinations (Tefera and Tana, 2002). The lower LERp in the S+H treatment might account for the intercropping system's reduced peanut yield (Fig. 2g, h), indicating that the semi-erect peanut–dwarf sorghum intercropping combination was more effective. Such disparities in yield outcomes mirror findings in sorghum-cowpea systems, where regional and cultivar variations dictate productivity (Moi et al., 2021) thereby underscoring the critical role of genotype selection and regional adaptability in optimizing intercropping performance. The yield advantage of intercropping system may stem from sorghum's strong competitive ability and peanuts' ecological niche compromise.

Morphological assessments revealed that intercropping, particularly S+L treatment, increased sorghum yield and growth (Supplementary Fig. 2 and Supplementary Fig. 3). However, intercropping induced an

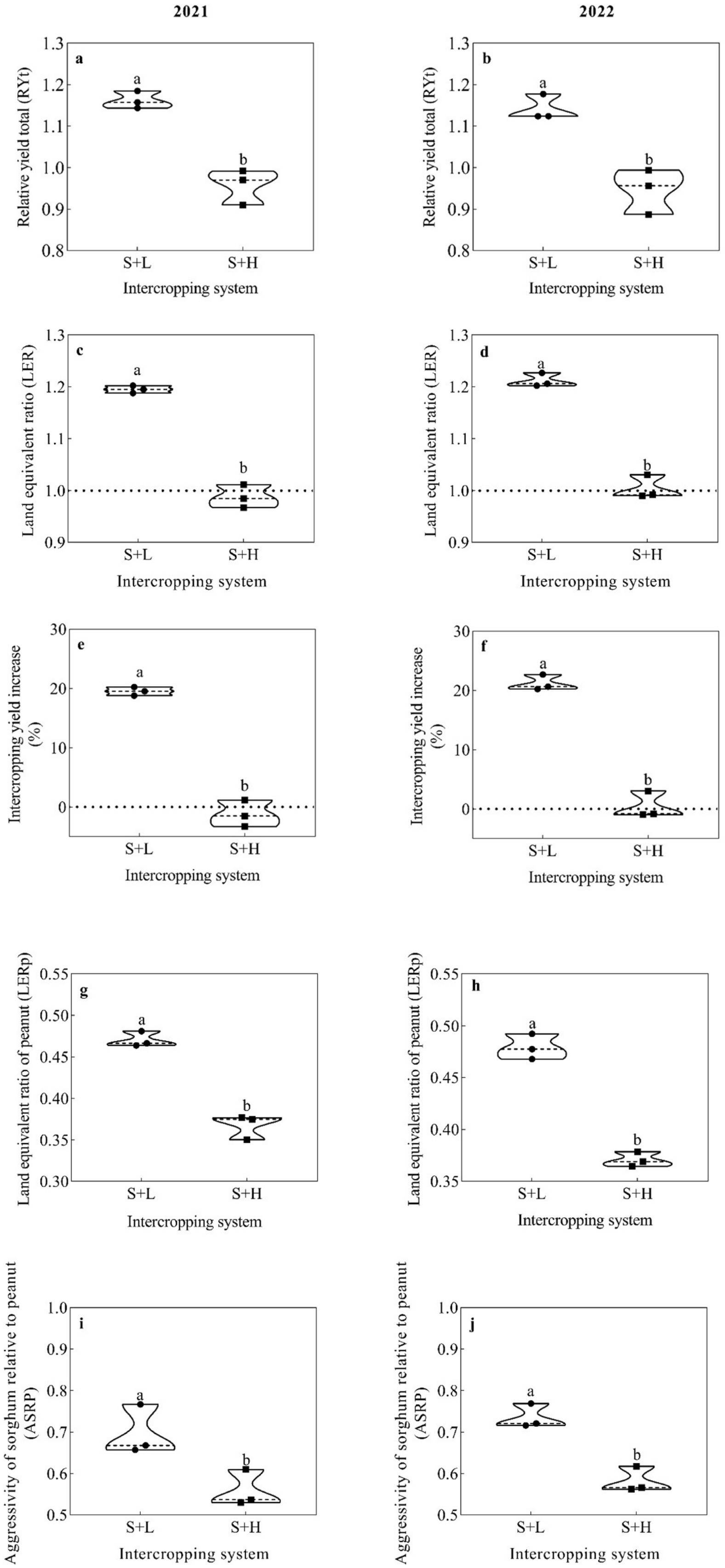

Fig. 2. Effects of intercropping on (a, b) relative yield total (RYt), (c, d) land equivalent ratio (LER), (e, f) percentage of intercropping yield increase, land equivalent ratio of peanut (LERp), and (i, j) aggressivity of sorghum relative to peanut (ASPR) in 2012 and 2022. Values are means ± SE (n = 3). Different letters indicate significant differences between sorghum/semi-erect type peanut intercropping (S+L) and sorghum/erect type peanut intercropping (S+H) at $P < 0.05$.

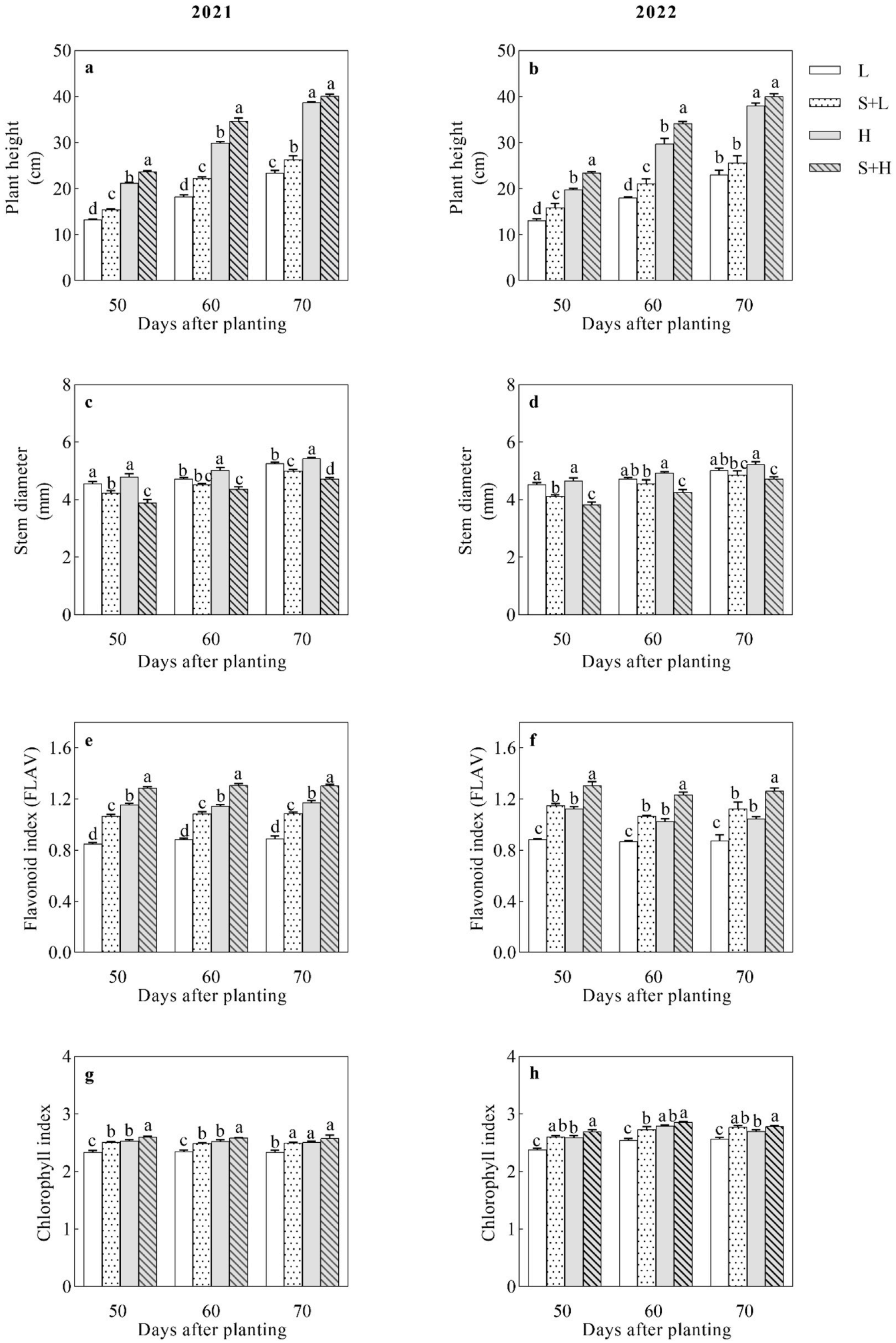

Fig. 3. Effects of intercropping on peanut (a, b) plant height, (c, d) stem diameter, (e, f) flavonoid index, and (g, h) chlorophyll index at 50, 60, and 70 days after planting in 2021 and 2022. Values are means ± SE (n = 3). Different letters indicate significant differences among treatments at $P < 0.05$. Treatments are as follows: L = semi-erect type peanut monocropping, S+L = sorghum/semi-erect type peanut intercropping, H = erect type peanut monocropping, and S+H = sorghum/erect type peanut intercropping, respectively.

imbalance in peanut development, characterized by increased plant height but reduced stem diameter (Fig. 3a–d), resulting in an imbalance in peanut growth and development. Shading caused by intercropping interferes with lignin synthesis and photosynthesis in dwarf crops, leading to weak stems and taller plants (Hussain et al., 2019). Peanut intercropped with sorghum exhibited slower growth than monocropped peanut (Fig. 2a, b), consistent with previous studies on maize–peanut (Li et al., 2019; Gao et al., 2022), sorghum–cowpea (*Vigna unguiculata*) (Parwada and Chinyama, 2021), and sorghum–lima bean (*Phaseolus lunatus*) (Darapuneni et al., 2018) intercropping systems. Collectively,

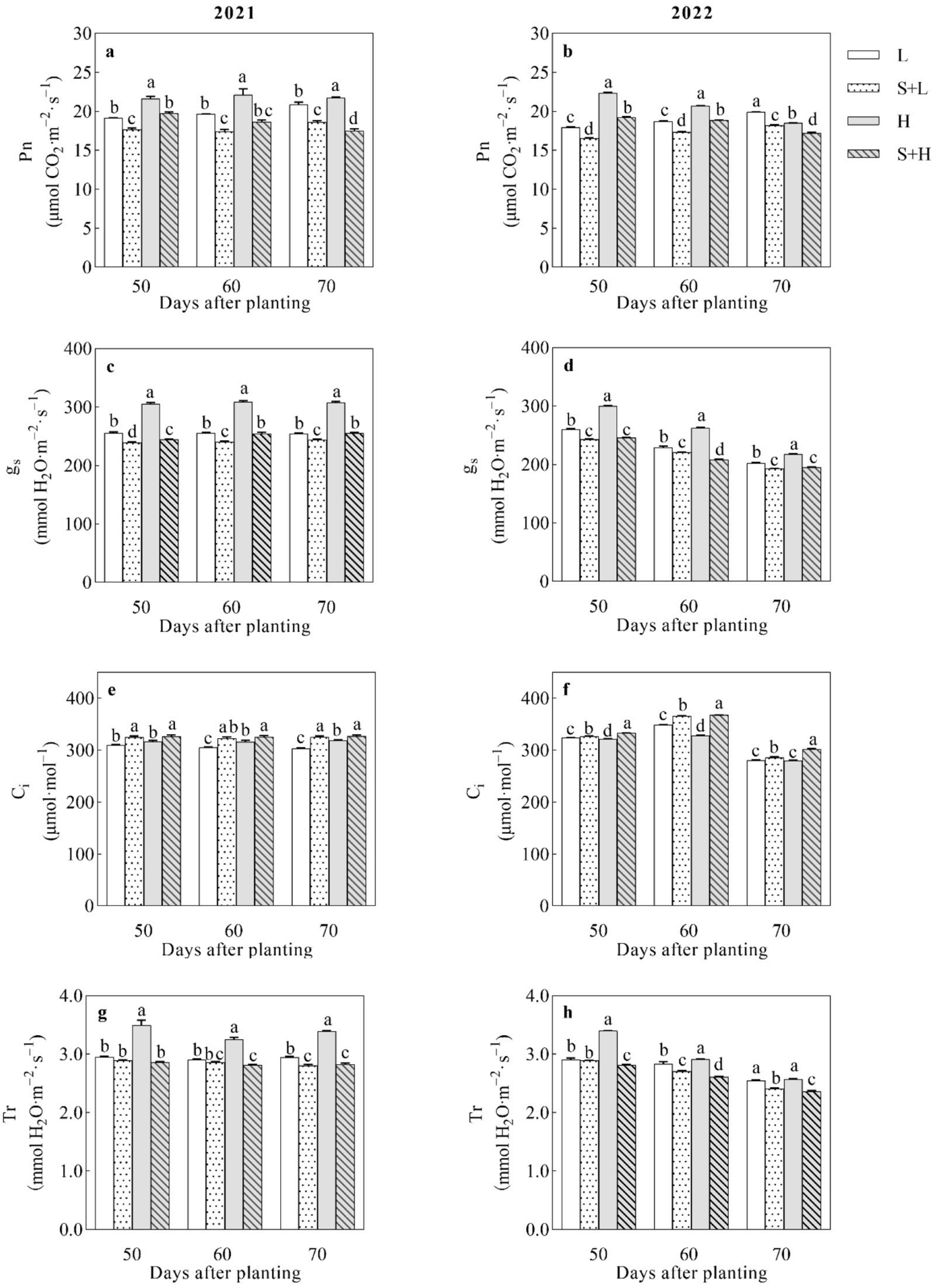

Fig. 4. Effects of intercropping on peanut (a, b) net photosynthetic rate (Pn), (c, d) stomatal conductance (g_s), (e, f) transpiration rate (Tr), and (g, h) intercellular CO_2 concentration (C_i) of peanut at 50, 60 and 70 days after planting in 2021 and 2022. Values are means ± SE (n = 3). Different letters indicate significant differences among treatments at $P < 0.05$. Treatments are as follows: L= semi-erect type peanut monocropping, S+L= sorghum/semi-erect type peanut intercropping. H = erect type peanut monocropping, and S+H= sorghum/erect type peanut intercropping.

these morphological structural alterations highlight a maladaptive morphological plasticity in peanut, reflecting a forced ecological niche compromise imposed by the competitive dominance of the sorghum canopy.

Analyses of relative yield total (Fig. 2a, b) and aggressiveness analyses (Fig. 2i, j) indicated that peanut plants encountered some inherent disadvantage in the intercropping system. RYt is widely used to assess comparatively growth advantages in intercropping systems (William, 1979; Wu et al., 2016). Our findings aligned with previous aggressivity analyses (Willey and Rao, 1980; Wu et al., 2016), where ASPR values above 0 (Fig. 2i, j) suggesting sorghum's stronger competitiveness. Peanut height and niche overlap significantly impacted competition and stability, with sorghum exhibiting increased competitiveness, particularly when grown with the semi-erect peanut. In intercropping, enhancing cereal growth was often prioritized and associated with reduced legume growth (Feng et al., 2021a). Thus, the overall productivity of the system appears to be driven by a cereal-biased competitive advantage, occurring at the expense of the vegetative suppression of the

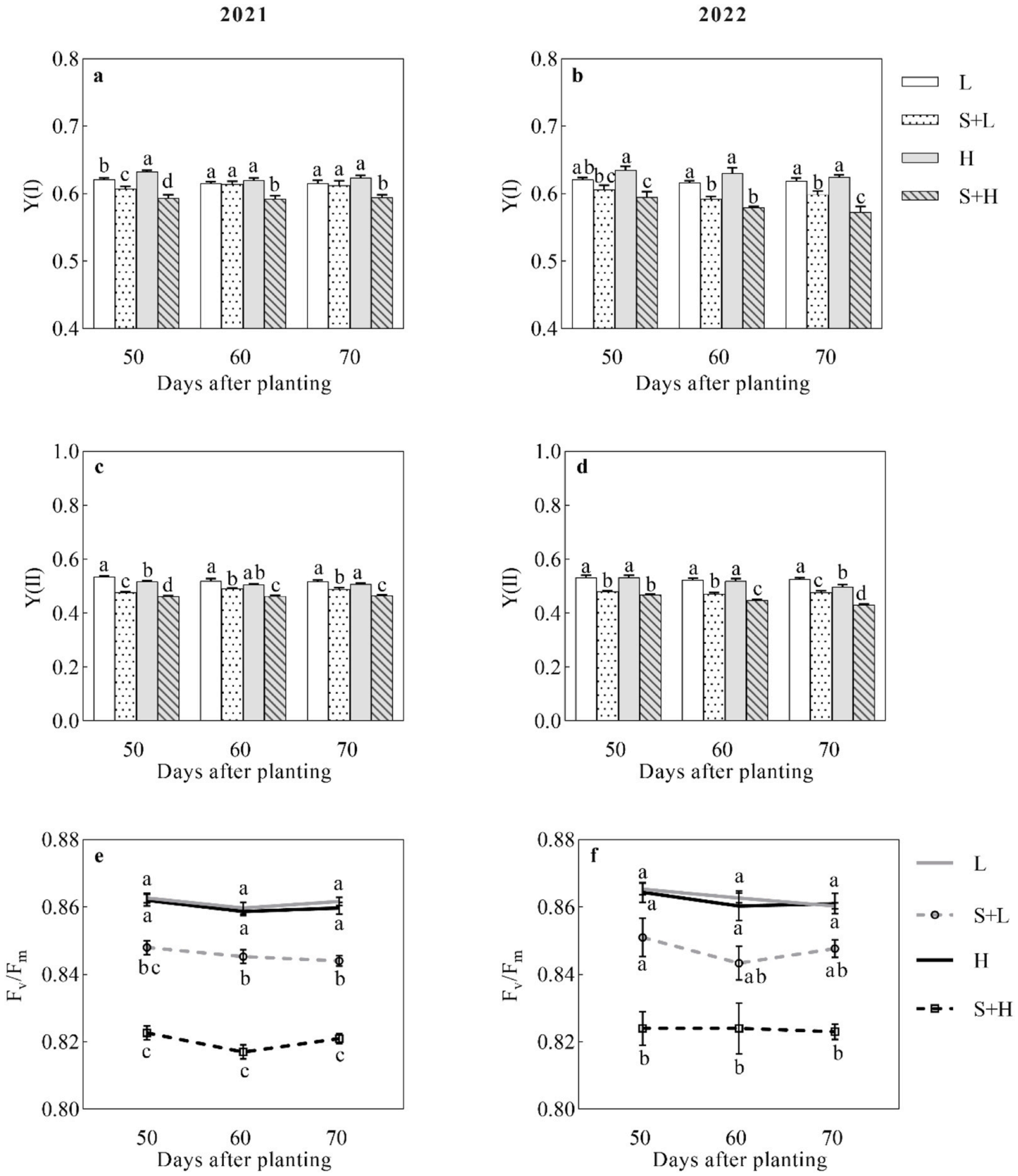

Fig. 5. Effects of intercropping on the (a, b) actual quantum yield of PSI [Y(I)], (c, d) actual quantum yield of PSII [Y(II)], and (e, f) maximum photochemical efficiency of PSII (F_v/F_m) in peanut leaves at 50, 60 and 70 days after planting in 2021 and 2022. Values are means ± SE (n = 3). Different letters indicate significant differences among treatments at $P < 0.05$.

intercropped legume.

Integrated analyses of photosynthetic gas exchange (Fig. 4), plant height (Fig. 3a, b), and yield (Fig. 2c–h) revealed divergent responses of the two peanut accessions to intercropping. Crop-specific traits are known to contribute significantly to intercropping success (Kiær et al., 2022). Consistent with studies on maize–peanut systems (Feng et al., 2021a; Han et al., 2022), we observed varied sensitivity among the peanut accessions. Unlike soybean, which adapts to intercropping with maize by increasing height (Zhang et al., 2023), peanut responded similarly in peanut-sorghum intercropping. Furthermore, while the erect peanut–sorghum system yielded more peanuts, the semi-erect system achieved superior overall productivity, suggesting greater resilience to competition and thereby underscoring the critical importance of crop-specific functional traits in intercropping designs.

4.2. *Response of the photoprotection mechanism in leaves of two peanut accessions to intercropping competitive disadvantage*

Photoinhibition is a key factor limiting crop productivity, and our results demonstrated that peanut-sorghum intercropping decreased Pn and photosystem activity (Fig. 5). These observations aligned with previous research, where Y(II) values declined in soybean–maize intercropping compared to monocultures (Yao et al., 2017). Intercropping generally introduces a dynamic environment of fluctuating shade and light, impacting crop growth—soybean growth, for example, is often compromised by inevitable shading from maize (Yao et al., 2017). Similar effects were noted in peanut–maize intercropping, where Pn in peanut declined while Y(II) and qP increased (Han et al., 2022). The peanut-sorghum intercropping system inevitably elicited two distinct responses in peanut leaves: (i) elevated NPQ with decreased PSII activity or (ii) reduced NPQ paired with enhanced PSII activity. This response shift was closely linked to light intensity variation (Yao et al., 2017). Shading intensity strongly influenced NPQ, with moderate shading

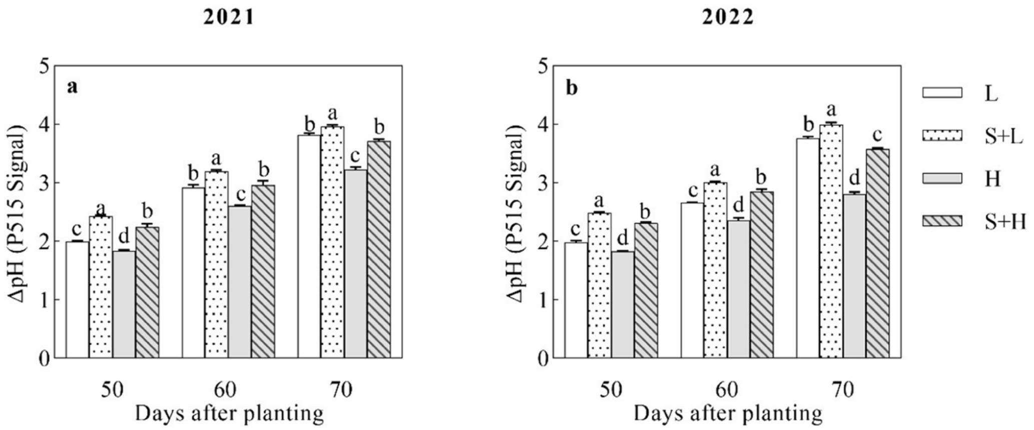

Fig. 6. Effects of intercropping on the proton gradient (ΔpH) in leaves of peanuts at 50, 60 and 70 days after planting in (a) 2021 and (b) 2022. Values are means ± SE (n = 3). Different letters indicate significant differences among treatments at $P < 0.05$. Treatments are as follows: L = semi-erect type peanut monocropping, S+L = sorghum/semi-erect type peanut intercropping, H = erect type peanut monocropping, and S+H = sorghum/erect type peanut intercropping.

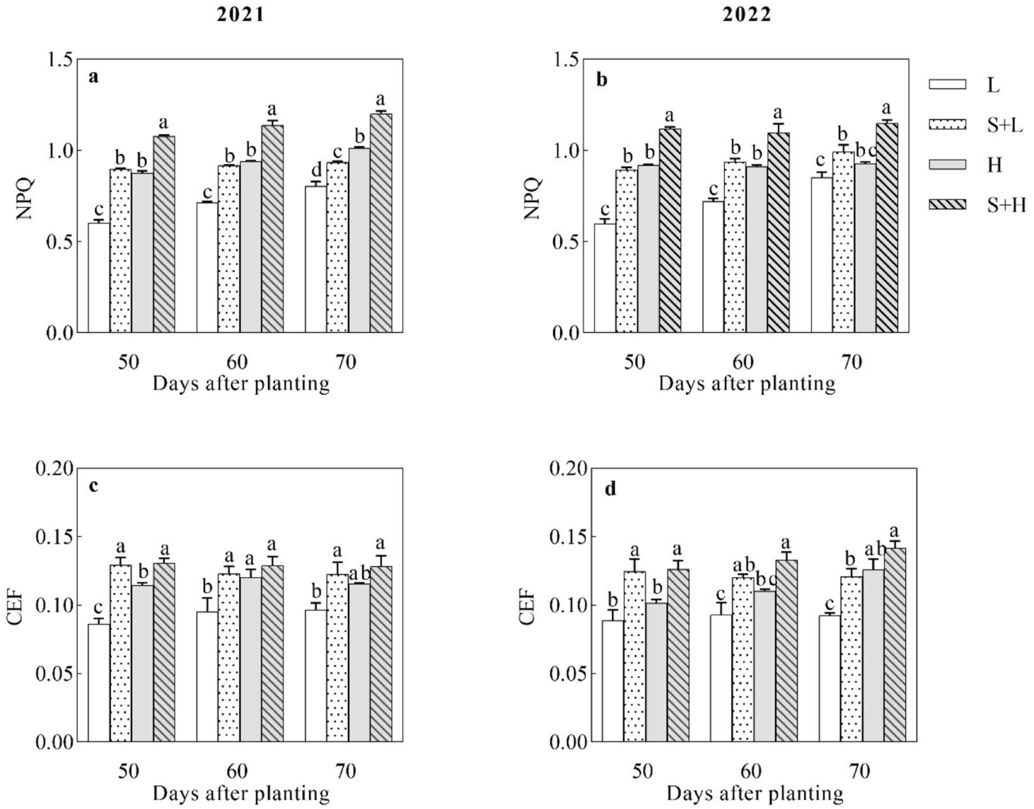

Fig. 7. Effects of intercropping on (a, b) non-photochemical quenching (NPQ) and (c, d) cyclic electron flow (CEF) in peanut leaves at 50, 60, and 70 days after planting in 2021 and 2022. Values are means ± SE (n = 3). Different letters indicate significant differences among treatments at $P < 0.05$. Treatments are as follows: L = semi-erect type peanut monocropping, S+L = sorghum/semi-erect type peanut intercropping, H = erect type peanut monocropping, and S+H = sorghum/erect type peanut intercropping.

increasing NPQ levels and intense shading reducing them (Dang et al., 2023). NPQ plays a protective role in dissipating excess excitation energy as heat (Erickson et al., 2015). In our experiment, the intercropped peanuts experienced moderate shading, necessitating increased NPQ to mitigate potential damage from surplus excitation energy on the photosystem.

Integrated analysis of photosystem parameters Y(I) (Fig. 5a, b), Y(II) (Fig. 5c, d), CEF (Fig. 7c, d), NPQ (Fig. 7a, b), and ΔpH (Fig. 6a, b) suggested that the photoprotection mechanisms played a key role in maintaining peanut foliar photosystem activity under intercropping. Intercropped peanut leaves exhibited elevated NPQ (Fig. 7a, b), consistent with studies that link increased NPQ with PSII photoinhibition and reduced photosynthetic carbon assimilation (Tikkanen et al., 2014). More recent research indicated that increased NPQ also enhances F_v/F_m and supports the repair of photosynthetic carbon fixation capacity (Kromdijk et al., 2016). Crucially, the enhanced ΔpH in intercropped leaves (Fig. 6a, b) indicates significant thylakoid lumen acidification, a prerequisite for energy dissipation (Ma et al., 2021b; Sun et al., 2023). Our findings also confirmed previous observations that higher NPQ correlated with increased ΔpH (Joliot and Johnson, 2011).

However, the response of NPQ to ΔpH varied between peanut accessions in this study. Rapidly reversible NPQ (qE), a key component of NPQ, is strongly influenced by ΔpH (Kromdijk et al., 2016; Ma et al., 2021a). CEF is an essential photoprotection mechanism for crop growth and development under stress (Song et al., 2020; Storti et al., 2020; Ma et al., 2021a; Sun et al., 2022) as it sustains ATP synthesis and contributes to maintaining ΔpH in thylakoids under photoinhibition (Yamamoto and Shikanai, 2018; Storti et al., 2020; Ma et al., 2021a; Sun et al., 2022, 2024). CEF facilitates proton accumulation in the thylakoid lumen at high ΔpH. The inhibition of two CEF pathways— (PGR5)/PRG5-like photosynthetic phenotype 1 (PGRL1), and chloroplast NAD(P)H dehydrogenase (NDH) —significantly reduces thylakoid ΔpH (Lu et al., 2020). Consequently, CEF functioned as a regulatory hub, ensuring the appropriate thylakoid ΔpH to modulate NPQ and mitigate the adverse effects of the complex light environment. Collectively, this CEF-driven photoprotective regulatory hub enhances the physiological resilience of peanut to intercropping-induced stress, thereby preserving the functional integrity and overall productivity of the system.

5. Conclusions

The intercropping of a dwarf sorghum cultivar with legumes (peanuts) increased the sorghum yield over two crop cycles. Additionally, the intercropping disadvantages brought about by the intrinsic peanut stature could be overcome by identifying suitable accessions (or varieties) with the appropriate habit. To restore the peanut yield loss within the peanut-sorghum intercropping system, the semi-erect peanut plants were able to improve the LER and restore peanut yield, while delivering better sorghum growth and yield. Specifically, the two peanut accessions exhibited different responses in CEF and ΔpH. The increased CEF and ΔpH helped to alleviate photoinhibition and growth reduction in the semi-erect type peanut accession in the peanut-sorghum system. Interestingly, peanut plants with greater resilience to photoinhibition were able to maintain photosynthetic capacity, supporting sorghum yield improvement while reducing peanut yield loss in this intercropping system. This study provided a foundation for optimizing the production of dwarf sorghum cultivar through intercropping with peanuts, offering better photoprotection, plausibly derived in part from its semi-erect habit.

CRediT authorship contribution statement

Siddique Kadambot: Writing – review & editing, Supervision, Conceptualization. **Hans Lambers:** Writing – review & editing, Supervision, Conceptualization. **Chunming Bai:** Writing – original draft, Investigation, Formal analysis, Data curation. **Huan Liu:** Investigation, Data curation. **Mingzhu Ma:** Investigation, Data curation. **Jiayin Pang:** Writing – review & editing, Conceptualization. **Salam Shaikh:** Data curation. **Yifei Liu:** Writing – review & editing, Supervision, Resources, Project administration, Funding acquisition, Conceptualization. **Zhiyu Sun:** Writing – review & editing, Writing – original draft, Conceptualization. **Jean Wan Hong Yong:** Writing – review & editing, Resources.

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Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at doi:10.1016/j.fcr.2026.110431.

Data availability

Data will be made available on request.

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