

# Effects of Intercropping and Arbuscular Mycorrhizal Fungus (AMF) Inoculation on Photosynthetic Characteristics of Ginger (*Zingiber officinale* Roscoe) During Rhizome Development

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**Abstract** [Objectives] This study was conducted to investigate the effects of intercropping and arbuscular mycorrhizal fungi (AMF) on the photosynthetic characteristics of ginger (*Zingiber officinale* Roscoe), and to analyze the correlations between photosynthetic pigments and photosynthetic parameters. [Methods] Using ‘Luoping Yellow Ginger’ and ‘King 336’ pepper as plant materials, a two-factor pot experiment was conducted with monoculture vs. intercropping and inoculation vs. non inoculation with the arbuscular mycorrhizal fungus *Funneliformis mosseae*. The effects of AMF inoculation and intercropping patterns on the net photosynthetic rate (Pn), stomatal conductance (Gs), transpiration rate (Tr), intercellular CO<sub>2</sub> concentration (Ci), and photosynthetic pigments of ginger were analyzed. [Results] The results showed that at 60 d of growth, AMF significantly increased the net photosynthetic rate, stomatal conductance, and transpiration rate of monoculture ginger ( $P < 0.05$ ). The enhancement of photosynthesis was dependent on improved stomatal opening and water use efficiency. However, no significant differences in photosynthetic pigment contents were observed. From 90 to 120 d, photosynthesis declined and intercellular CO<sub>2</sub> concentration increased, indicating a shift in photosynthetic limitation from stomatal to non stomatal factors. In the intercropping with AMF treatment, Pn decreased significantly. Correlation analysis indicated that AMF and intercropping weakened the association between photosynthetic pigments and photosynthetic performance. In summary, AMF inoculation and cropping patterns can regulate the photosynthetic characteristics of ginger, and this regulation depends on stomatal behavior and growth stage dynamics. [Conclusions] This study provides a theoretical reference for research on the photosynthetic characteristics of ginger.

**Key words** Arbuscular mycorrhizal fungus; Intercropping; Ginger; Photosynthetic characteristic

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Ginger (*Zingiber officinale* Roscoe) is an economically and functionally significant crop worldwide. It is widely used in the flavor, pharmaceutical, and health supplement industries, with its market demand continuing to grow<sup>[1]</sup>. The yield and quality of ginger rhizomes depend primarily on the photosynthetic capacity of the plant during its development stage. At this stage, the leaf area of the plant reaches its peak, and the accumulation of photosynthetic products directly determines the rate of rhizome enlargement and the final yield<sup>[2]</sup>. During this period, ginger exhibits vigorous metabolism and is highly sensitive to environmental conditions and changes in rhizosphere nutrition. Adjustments in cultivation practice can significantly affect its photosynthetic efficiency and carbon assimilation capacity<sup>[3]</sup>.

Arbuscular mycorrhizal fungi (AMF) expand the root absorption range through their hyphal network, significantly enhancing the host plant's uptake efficiency of water and mineral nutrients (especially phosphorus), thereby improving leaf stomatal regulation and photosynthetic carbon assimilation capacity<sup>[4]</sup>. Previous

studies have shown that AMF inoculation can enhance net photosynthetic rate (Pn) by increasing stomatal conductance (Gs) and promoting CO<sub>2</sub> diffusion into leaves<sup>[5]</sup>. However, the regulatory effects of AMF on photosynthetic parameters of ginger at different growth stages and their relationship with stomatal characteristics have not been systematically investigated.

Intercropping systems can alleviate high-light stress to a certain extent and promote resource complementarity between crops by optimizing canopy structure and light distribution<sup>[6]</sup>. When ginger is intercropped with pepper, the shading effect of pepper may create a more favorable light environment for ginger. However, interspecific competition may also affect the functionality of the AMF symbiosis<sup>[7]</sup>. Currently, research on the synergistic effects of intercropping and AMF on the photosynthetic characteristics of ginger remains limited. In particular, the relative mechanisms of stomatal regulation and photosynthetic pigments under different treatments are still unclear.

Therefore, in this study, different measurement periods were set during the rhizome growth stage of ginger to analyze the effects of AMF inoculation and intercropping patterns on Pn, Gs, transpiration rate (Tr), intercellular CO<sub>2</sub> concentration (Ci), and photosynthetic pigments of ginger, and the correlation between photosynthetic pigments and photosynthetic parameters was also explored. This study aimed to elucidate the effects of intercropping

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and AMF on the photosynthetic characteristics of ginger and to provide a theoretical reference for research on ginger photosynthesis.

## Materials and Methods

### Experimental materials

The ginger cultivar used in this study was ‘Luoping Yellow Ginger’, and the pepper cultivar was ‘King 336’. The soil was collected from farmland in Weixinghu Street, Yongchuan District, Chongqing, at a depth of 0–20 cm. The soil samples were air-dried and sieved through a 2 mm sieve to remove gravel and plant residues. The inoculum consisted of *Funneliformis mosseae*, provided by the Microbiology Research Institute, Guangxi Academy of Agricultural Sciences. White clover (*Trifolium repens* L.) was used as the host plant and was propagated in sterilized substrate for three months. The inoculum contained hyphae, spores, and colonized roots, with approximately 100 spores per 10 g of soil.

### Experimental design

The experiment was conducted in a greenhouse at Chongqing University of Arts and Sciences under natural light conditions. A completely randomized design with two factors, *i. e.*, cropping pattern (ginger monoculture, pepper monoculture, and ginger-pepper intercropping) and AMF inoculation (inoculated and non-inoculated), was adopted, resulting in six treatments with 12 replicates per treatment. The substrate consisted of agricultural soil, perlite, and peat at a ratio of 5 : 3 : 2, with 10 kg of substrate per nutrition pot (40 cm × 40 cm pots). For the inoculated treatment, 700 g of AMF inoculum was applied, while the non-inoculated treatment received an equal amount of sterilized inoculum. Ginger pieces weighing 50 g with 3–4 full bud points were disinfected with 10% H<sub>2</sub>O<sub>2</sub>, and pepper seedlings (15 cm tall, healthy plug seedlings) were used. In the monoculture pattern, each pot contained two pieces of ginger or two pepper plants. In the intercropping pattern, each pot contained one piece of ginger and one pepper plant. After planting, the substrate was watered at 13% of its mass, and soil moisture was maintained at 70%–80% of field capacity during the growth period.

### Measurement indicators and methods

Starting from the 60<sup>th</sup> day after planting, sampling was conducted every 30 d for a total of three times (on days 60, 90, and 120). The third or fifth fully expanded functional leaf from the top was selected for measurement. Measurements were taken on clear windless mornings between 9:00 and 11:00 a. m. using an LI6400XT portable photosynthesis system to determine Pn, [ $\mu\text{mol}/(\text{m}^2 \cdot \text{s})$ ], Gs, [ $\text{mol}/(\text{m}^2 \cdot \text{s})$ ], Tr [ $\text{mmol}/(\text{m}^2 \cdot \text{s})$ ], and Ci ( $\mu\text{mol}/\text{mol}$ ). Each leaf was measured three times, and the average value was calculated. Before measurement, the leaf was allowed to stabilize in the cuvette for 2–3 min until the reading fluctuations were less than 5%.

Chlorophyll and carotenoid contents were extracted using 80% acetone<sup>[8]</sup>. Chlorophyll a (Chl a), chlorophyll b (Chl b) and carotenoid (Car) contents were calculated according to the

formulas of Lichtenthaler.

### Data processing and analysis

The data were statistically analyzed using SPSS 27.0 software. A two-way repeated-measures ANOVA was performed on the photosynthetic parameters of ginger to analyze the effects of different treatments and different sampling times. Chlorophyll content was analyzed by oneway ANOVA to compare differences among treatments. Spearman correlation analysis was used to examine the relationships between photosynthetic pigments and photosynthetic parameters. All figures were generated using Origin 2025 software.

## Results and Analysis

### Dynamic changes in photosynthetic parameters of ginger at different growth stages

Two-way ANOVA showed that treatment, growth stage (60, 90, and 120 d), and their interaction had significant effects on the Pn, Gs, Tr, and Ci of ginger leaves ( $P < 0.05$ ). All photosynthetic parameters exhibited clear dynamic changes with the growth process (Fig. 1). The Pn values differed significantly among treatments. In the monoculture treatment with AMF inoculation (G-AMF), Pn peaked at 120 d and was higher than in the monoculture treatment without AMF inoculation (G-NAMF) and the intercropping treatment with AMF inoculation (I-AMF), indicating a potential enhancement of photosynthetic capacity by AMF inoculation in monoculture ginger. In the I-AMF treatment, Pn was relatively high at 60 d and slightly higher than that in G-AMF, but decreased as the growth stage progressed, suggesting that its photosynthetic advantage was concentrated at 60 d. Gs and Tr exhibited a consistent trend, rising or remaining stable with the advancement of the growth stage. At 120 d, Gs and Tr in the G-AMF treatment were significantly higher than those in the G-NAMF treatment ( $P < 0.05$ ), indicating that AMF inoculation can improve gas exchange and water metabolism in monoculture ginger. In the I-AMF treatment, Pn decreased at 120 d, but Gs did not decrease correspondingly, suggesting that stomatal limitation was not the dominant factor for the decline in Pn. Ci showed a continuous increasing trend at 60, 90, and 120 d, with the most significant differences observed at 120 d. The Ci value in the G-AMF treatment reached approximately 850  $\mu\text{mol}/\text{mol}$  at 120 d, which was significantly higher than those in other treatments ( $P < 0.05$ ). At 120 d, the Pn value in the G-AMF treatment did not show a significant increase, while in the I-AMF treatment, Pn decreased, but Ci remained at a relatively stable high level.

### Effects of intercropping and AMF inoculation on chlorophyll content

The effects of different cropping patterns and AMF inoculation on the photosynthetic pigment content of ginger leaves were generally minor, with differences between most treatments not reaching statistical significance ( $P > 0.05$ ). However, significant differences were observed at specific time points (Table 1). At 60

and 90 d, there were no significant differences in Chl a, Chl b, or Car content between treatments. At 60 d, the I-AMF treatment had the highest Chl a content (2.12 mg/g), while the I-NAMF treatment had the lowest (1.56 mg/g) value, suggesting that AMF inoculation under intercropping may promote pigment synthesis at the early stage, although the differences were not statistically significant.

As the growth stage progressed to 120 d, the photosynthetic pigment content showed clear differentiation. In the monoculture treatment with AMF inoculation (G-AMF), Chl a significantly decreased to 1.70 mg/g at 120 d, which was significantly lower than that in other treatments ( $P < 0.05$ ). Its Chl b and Car showed similar decreasing trends. In contrast, the monoculture treatment without AMF inoculation (G-NAMF) and the intercropping treatment without AMF inoculation (I-NAMF) both exhibited a relatively high capacity for pigment maintenance at 120 d. Notably, in the I-NAMF treatment, Chl a increased from 1.56 mg/g at 60 d to 2.10 mg/g at 120 d, representing an increase of 34.6%, suggesting that under the condition of intercropping without AMF inoculation, ginger leaves may display either delayed pigment accumulation or enhanced resistance to senescence.

Although AMF inoculation significantly increased Pn under monoculture, the contents of Chl a, Chl b, and Car all decreased, indicating that the increase in photosynthetic rate was not driven by increased pigment content. In the intercropping without AMF inoculation (I-NAMF) treatment, photosynthetic pigments accumulated significantly at 120 d, showing a marked increase compared with the levels at 60 d.

**Table 1** Changes in photosynthetic pigment contents of ginger under different treatments (Mean  $\pm$  SD)

| Growth stage | Treatment | Chl a//mg/g       | Chl b//mg/g       | Car//mg/g         |
|--------------|-----------|-------------------|-------------------|-------------------|
| 60 d         | G-AMF     | 1.89 $\pm$ 0.66 a | 0.60 $\pm$ 0.25 a | 3.27 $\pm$ 1.12 a |
|              | G-NAMF    | 1.93 $\pm$ 0.74 a | 0.66 $\pm$ 0.29 a | 3.29 $\pm$ 1.30 a |
|              | I-AMF     | 2.12 $\pm$ 0.80 a | 0.68 $\pm$ 0.26 a | 3.66 $\pm$ 1.16 a |
|              | I-NAMF    | 1.56 $\pm$ 0.71 a | 0.54 $\pm$ 0.22 a | 2.58 $\pm$ 1.36 a |
| 90 d         | G-AMF     | 1.76 $\pm$ 0.40 a | 0.59 $\pm$ 0.13 a | 3.11 $\pm$ 0.70 a |
|              | G-NAMF    | 1.91 $\pm$ 0.33 a | 0.64 $\pm$ 0.14 a | 3.37 $\pm$ 0.59 a |
|              | I-AMF     | 1.84 $\pm$ 0.67 a | 0.61 $\pm$ 0.21 a | 3.41 $\pm$ 0.88 a |
|              | I-NAMF    | 1.84 $\pm$ 0.41 a | 0.64 $\pm$ 0.14 a | 3.22 $\pm$ 0.71 a |
| 120 d        | G-AMF     | 1.70 $\pm$ 0.28 b | 0.60 $\pm$ 0.10 b | 3.07 $\pm$ 0.51 b |
|              | G-NAMF    | 1.87 $\pm$ 0.46 a | 0.62 $\pm$ 0.16 a | 3.42 $\pm$ 0.82 a |
|              | I-AMF     | 1.71 $\pm$ 0.66 a | 0.59 $\pm$ 0.21 a | 3.31 $\pm$ 1.02 a |
|              | I-NAMF    | 2.10 $\pm$ 0.38 a | 0.72 $\pm$ 0.12 a | 3.84 $\pm$ 0.73 a |

Different lowercase letters indicate significant differences between treatments ( $P < 0.05$ ).

### Correlation analysis between photosynthetic pigments and photosynthetic parameters

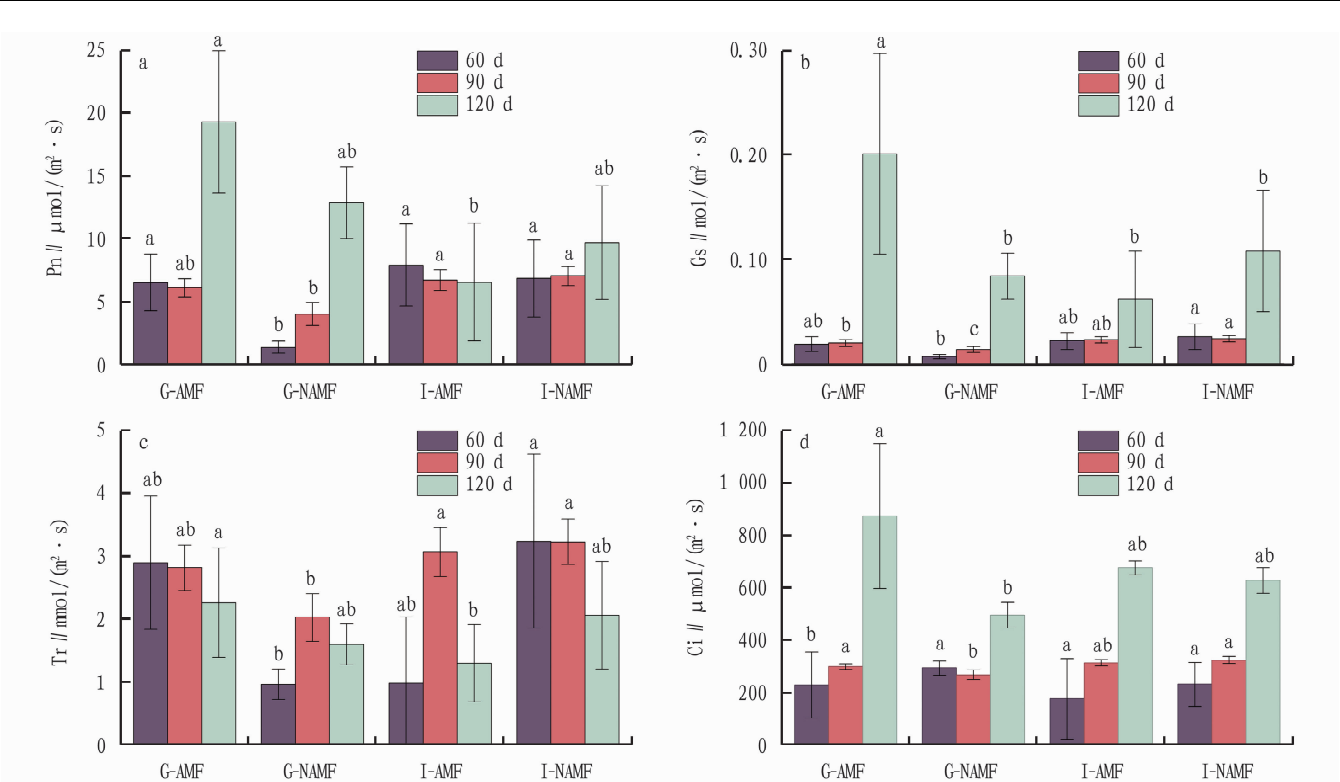
Under different cropping patterns and AMF inoculation treatments, the correlations of Pn with various photosynthetic parameters

and photosynthetic pigments in ginger showed significant differences. The results indicated that in all treatments, photosynthetic pigments were significantly and positively correlated with each other ( $r_s \geq 0.78$ ,  $P < 0.01$ ). In the G-AMF treatment, the correlations between Chl a and Chl b ( $r_s = 0.82$ ), Chl a and Car ( $r_s = 0.98$ ), as well as Chl b and Car ( $r_s = 0.78$ ), were all extremely significant. In the G-NAMF treatment, these correlations were even stronger ( $r_s = 0.96 - 0.98$ ,  $P < 0.01$ ). In the I-AMF and I-NAMF treatments, the pigments also maintained highly significant positive correlations ( $r_s \geq 0.90$ ,  $P < 0.01$ ), indicating that the photosynthetic pigment system exhibits a highly stable, synergistic pattern of variation that is unaffected by either cropping pattern or mycorrhizal inoculation.

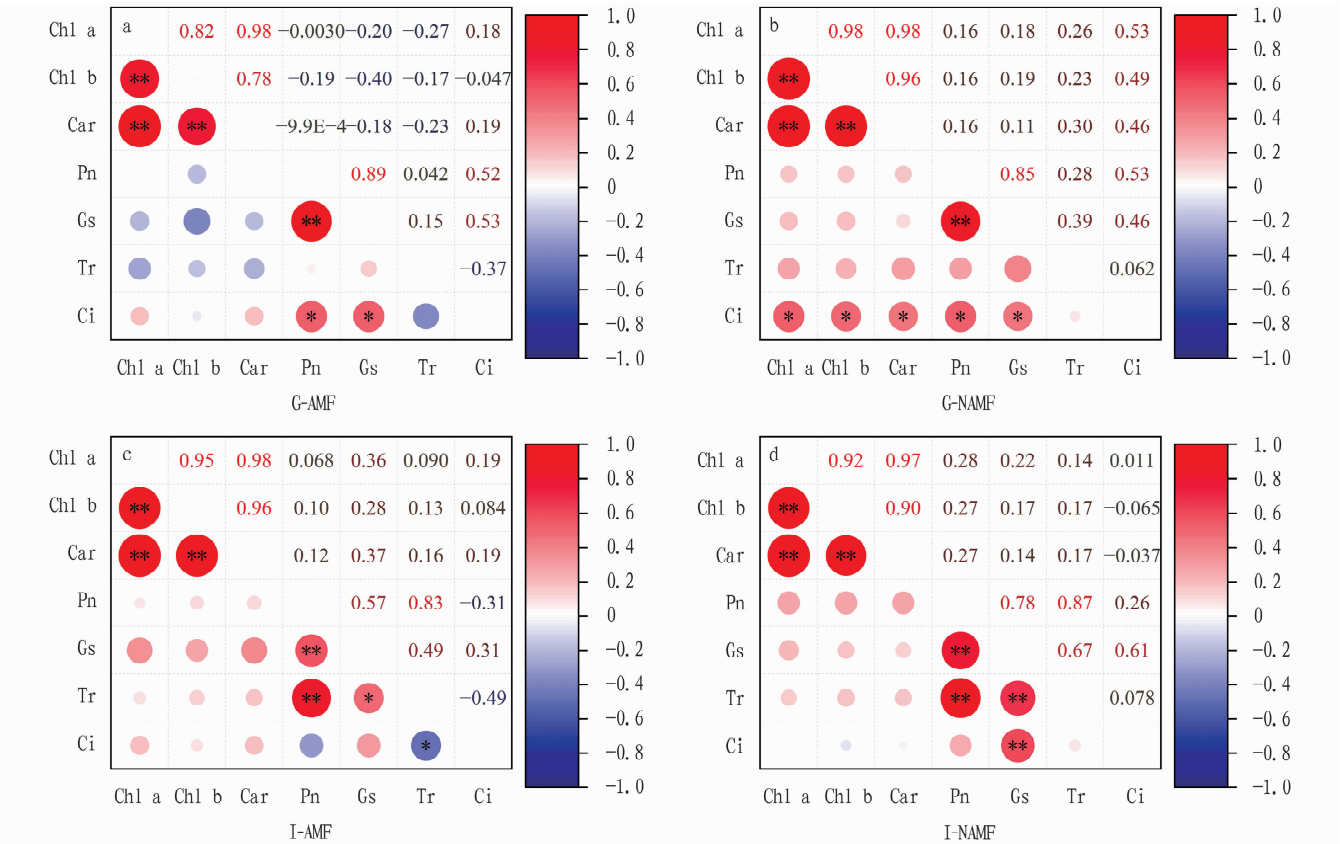
The correlations between gas-exchange parameters showed clear treatment-dependence. In the G-AMF treatment, Pn was found to be in an extremely significant positive correlation with Gs ( $r_s = 0.89$ ,  $P < 0.01$ ). Similarly, positive correlations were also significant between Pn and Ci ( $r_s = 0.52$ ) and Gs and Ci ( $r_s = 0.53$ ) ( $P < 0.05$ ). In the G-NAMF treatment, Gs was in an extremely significant positive correlation with Ci ( $r_s = 0.85$ ,  $P < 0.01$ ), and Pn was significantly positively correlated with Ci ( $r_s = 0.53$ ,  $P < 0.05$ ). In the I-AMF treatment, Pn showed a highly significant positive correlation with Tr ( $r_s = 0.83$ ,  $P < 0.01$ ), and a significant positive correlation with Gs ( $r_s = 0.57$ ,  $P < 0.05$ ), while a significant negative correlation was found between Tr and Ci ( $r_s = -0.49$ ,  $P < 0.05$ ). In the I-NAMF treatment, four pairs of parameters, including Pn and Tr ( $r_s = 0.87$ ) and Pn and Gs ( $r_s = 0.78$ ), all exhibited highly significant positive correlations ( $P < 0.01$ ). Under monoculture with AMF inoculation, the Pn-Gs correlation was the strongest, whereas under intercropping, the Pn-Tr correlation was more prominent.

The correlations between photosynthetic pigments and gas exchange parameters were generally weak. Only in the G-NAMF treatment were Chl a ( $r_s = 0.53$ ), Chl b ( $r_s = 0.49$ ), and Car ( $r_s = 0.46$ ) significantly positively correlated with Ci ( $P < 0.05$ ). None of other combinations showed significant correlations ( $P > 0.05$ ). In the G-AMF, I-AMF, and I-NAMF treatments, no significant correlations were found between the two sets of indicators ( $P > 0.05$ ), and most absolute correlation coefficients were below 0.30, indicating a low degree of correlation between them.

Overall, the distribution of significant correlations varied markedly among the four treatments. The G-NAMF treatment was the only one in which significant correlations between pigments and gas exchange parameters were observed. The correlations were weakened after AMF inoculation or intercropping. That is to say, the correlations among gas exchange parameters exhibited treatment specificity, indicating that cropping patterns and mycorrhizal inoculation not only affect individual physiological indicators, but also alter the correlation structure among variables.



Different lowercase letters indicate significant differences between treatments at the 0.05 level; and the same letter indicates no significant difference.  
**Fig. 1** Dynamic changes in photosynthetic physiological indicators of ginger under different cropping patterns with growth stages



\*\* indicates  $P < 0.01$ , and \* indicates  $P < 0.05$ .

**Fig. 2** Correlation between photosynthetic pigments and photosynthetic parameters

## Conclusion and Discussion

The results of this study indicate that AMF inoculation and cropping patterns exhibit regulatory effects on the photosynthetic characteristics of ginger, and that the underlying regulatory mechanisms differ considerably among various treatments. In the monoculture treatment with AMF inoculation (G-AMF), the highest net photosynthetic rate (Pn) was observed at 120 d, and it was significantly higher than that in other treatments. This peak was accompanied by concurrent significant increases in stomatal conductance (Gs) and transpiration rate (Tr), indicating that AMF can enhance the photosynthetic capacity of monoculture ginger by improving stomatal conductance and promoting water metabolism, thereby creating favorable conditions for photosynthesis<sup>[9]</sup>.

However, in the intercropping treatment with AMF inoculation (I-AMF), although Pn was relatively high at 60 d, it continuously decreased as the growth stage progressed, whereas Gs did not decline correspondingly. It suggests that stomatal limitation was not the primary cause of the decrease in Pn under this treatment. It is speculated that the decline might be closely related to dynamic changes in photosynthetic pigments and constraints on carbon metabolism. The Ci increased with the growth stage in all treatments. In the I-AMF treatment, Pn decreased while Ci remained high, further confirming that the limitation to photosynthesis had shifted to biochemical reactions or metabolic processes rather than stomatal factors<sup>[10]</sup>.

Analysis of the dynamic changes in photosynthetic pigments showed that AMF inoculation did not increase chlorophyll content under monoculture and even led to a significant decrease at 120 d. However, Car content was positively correlated with Pn, suggesting that Car may play a key role in maintaining or enhancing the photosynthetic rate of monoculture ginger<sup>[11]</sup>. In the intercropping treatment without AMF inoculation (I-NAMF), photosynthetic pigments accumulated markedly at 120 d, accompanied by an increase or stabilization of Pn. This suggests that the intercropping pattern itself may delay leaf senescence and enhance pigment retention, thereby supporting sustained photosynthetic performance<sup>[12]</sup>.

Correlation analysis revealed that the relationships between photosynthetic pigments and gas exchange parameters varied considerably with different treatments, reflecting the plasticity of plant physiological regulation. In all treatments, Chl a, Chl b and Car were significantly positively correlated with each other, demonstrating the stable synergistic nature of the lightharvesting system. Under monoculture with AMF inoculation, Pn was significantly correlated with Gs, whereas under intercropping, the correlation between Pn and Tr was stronger. A significant association between pigments and gas exchange parameters was observed only in the noninoculated treatments, primarily as a positive correlation with Ci. Both AMF inoculation and intercropping significantly weakened this association, further revealing that the mechanisms by which AMF regulates ginger photosynthesis differ fundamentally under different cropping patterns<sup>[13]</sup>.

This study demonstrated that AMF inoculation and cropping patterns significantly influence the photosynthetic characteristics and pigment dynamics of ginger. Under monoculture, AMF inoculation enhanced the photosynthetic rate by improving stomatal conductance and water metabolism, independent of photosynthetic pigment accumulation. Under intercropping, the positive effect of AMF on photosynthesis was limited. The intercropping treatment without AMF inoculation delayed leaf senescence and stabilized photosynthesis through pigment accumulation in the later growth stage. The correlations between photosynthetic pigments were stable, whereas the correlations between gas exchange parameters and those between pigments and gas exchange parameters were influenced by cropping patterns and mycorrhizal inoculation.

In summary, AMF and cropping patterns influence the photosynthetic efficiency of ginger by regulating stomatal behavior, metabolism, and pigment accumulation. This study provides a theoretical basis for optimizing ginger cultivation and the rational utilization of microorganisms.

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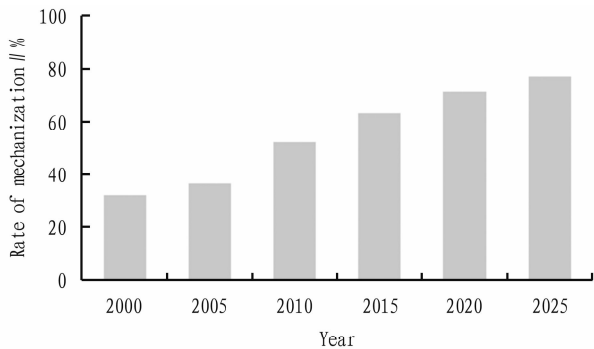
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machine-operators to improve the quality of outsourcing service in China.

### Modernizing mechanical equipment and support

Technology develops in an unprecedented speed nowadays. The rate of agricultural mechanization in plowing, planting and harvesting for some most important crops in China has soared from 32% in 2000 to 76.7% in 2025 (Fig. 5). Machine substituting for human labor has become an inevitable trend in modern agriculture globally.



Data were adopted from the official reports.

**Fig. 5** Rate of agricultural mechanization in plowing, planting and harvesting for the most important crops in China during 2000 to 2025

The flourishing of artificial intelligence-based technology propels the agricultural mechanization even further. China is now making tremendous progress in vision-guidance, robotic systems, AI-based control units and equipment. Prospectively, a highly promoted production efficiency in agriculture driven by integrating mega data and ‘AI for machine’ is to be realized and in such a system, precise harvesting will be achieved for variable and delicate crops with the least grain yield losses and quality deterioration.

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