

Expanding crop adaptability to increase planting area: a promising strategy for enhancing agricultural production

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Abstract

The yield gap accurately measures the efficiency of converting the maximum genetic yield into the average yield per unit area, nationally or globally. However, despite continuous advancements in breeding and cultivation technology, the yield gap continues to widen in many regions worldwide. Our findings suggest that widespread planting of high-yielding varieties can enhance crop yield per unit area and narrow the yield gap, thereby offering an effective strategy to convert the potential high yield per plant into an overall increase in production.

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Introduction

Millions of people worldwide struggle with food insecurity and hunger, a problem exacerbated by the ongoing effects of COVID-19^[1,2]. To secure global food supplies by 2050, it is estimated that average crop production must increase by approximately 60%^[3,4]. One way to address this challenge is to increase crop yield per unit area of land, thereby reducing the pressure of sustained population growth without expanding agricultural land. Innovations in germplasm resources, such as ideotype breeding or plant architecture modifications, can increase productivity and meet the rapidly growing demand for food grain production^[5,6]. For instance, the Green Revolution increased the yield of crop species such as wheat, rice, and maize through the introduction of semi-dwarf traits^[6,7]. Semi-dwarf breeding to increase yield potential is a type of ideotype breeding or modification of plant architecture^[8]. Developing an ideal rice architecture with a smaller tiller number and more grains per panicle has been proposed as a means to increase rice yield potential^[9,10]. In addition, heterosis breeding has been utilized to enhance rice yield potential, creating rice hybrids with 10%–20% higher yields than conventional varieties, which have been grown commercially in China since the 1970s.

Additionally, varieties resistant to multiple diseases, such as blast, bacterial blight, grassy stunt, and insects like brown planthopper, green leafhopper, stemborer, and gall midge have helped stabilize the world rice production^[6,11]. Innovations in germplasm resources, including the development of ideal plant architecture, heterosis, and resistance to biotic and abiotic stresses, often result in a comprehensive increase in crop yield by improving the yield potential per plant. However, how the

high-yield potential per plant is efficiently translated into an overall increase in production is rarely addressed. The yield gap accurately measures the efficiency of converting the maximum genetic yield into the average yield per unit area, globally or nationally. Despite these advances in agricultural research, however, differences between yields obtained in research stations and those achieved by farmers in the field persist in many nations, finally causing yield gaps to widen^[12,13].

The concept of wide adaptation as a breeding trait is not frequently referenced^[6]. However, crop varieties with this attribute have the potential for rapid expansion of their cultivation areas. For instance, the semi-dwarf rice variety IR8, released by the International Rice Research Institute (IRRI) in 1966, produced twice the yield of traditional varieties when grown under irrigation and became widely cultivated in various rice-growing regions of Asia, Africa, and Latin America, earning it the moniker 'miracle rice'^[6]. Similarly, the Chinese hybrid rice super variety Shanyou63, grown on 90 million mu from 1984 to 2012 in China, showed wide adaptability^[14]. We showed previously that growing Shanyou63, a variety with gradual daylength sensing capability, according to optimum cropping modes, enhanced its capacity for multi-latitude adaptation^[15]. However, whether wide adaptability can affect yield efficiency of crop varieties had not been confirmed. Here, we developed a statistical model to quantify the contributions of variety yield and planting area to overall crop yield efficiency for rice, maize, soybean, and wheat. Our results support the hypothesis that expanding the cultivation area of high-yielding varieties can improve crop yield per unit area and close the yield gap, offering a strategy for increasing crop yield efficiency through wide adaptation.

Materials and methods

Data sources and data preprocessing

The data for rice, maize, soybean, and wheat variety information (variety name, approval year, approval province, unit area yield [the average yield from all trial regions], plant height, disease resistance, etc.) came from A-Seed (www.a-seed.cn). Data for the variety planting area (variety name and planting area for each year) came from the China Seed Industry Big Data Platform (<http://202.127.42.145/bigdataNew/home/ManageOrg>). The intersection of crop variety information and variety planting area was used as the crop variety dataset. Information about total sowing area, sowing area in each province, national crop unit area yield, and crop unit area yield in each province came from the National Bureau of Statistics (www.stats.gov.cn). Data for crop yield of different countries came from the Food and Agriculture Organization of the United Nations, FAO (www.fao.org/home/en).

Modeling the planting area–enhanced production theory

Definition the model parameters of the theory

The *yield rate* is used to measure the rate of change of unit area yield. Since the yield fluctuates greatly between consecutive years, if the *yield rate* between these years is used, the background noise will be large. Therefore, to remove the background noise, the *yield rate* is calculated over a 5-year sliding window. Here, \bar{y}_A represents the average unit area yield of the previous 5 years, and \bar{y}_B represents the average unit area yield of the next 5 years.

$$\text{yield rate}_i = \frac{\bar{y}_B - \bar{y}_A}{\bar{y}_A}$$

r_{area} is the ratio between the planting area of the crop with the largest planting area (Area_1) and the total planting area (Total area) for each year. Area_1 represents the planting area of the variety, and Total area refers to the cultivated area of the crop.

$$r_{\text{area}} = \frac{\text{Area}_1}{\text{Total area}}$$

We use r'_{area} to represent the area share of a given variety.

$$r'_{\text{area}} = \frac{\text{Area}_{\text{variety}}}{\text{Total area}}$$

We approximate the average yield of the top five varieties (\bar{y}_{Top5}) as the maximum genetic yield of the year. r_{yield} is defined as the average yield of the top five varieties (\bar{y}_{Top5}) divided by the weighted average yield of all other varieties (\bar{y}_{other}).

$$r_{\text{yield}} = \frac{\bar{y}_{\text{Top5}}}{\bar{y}_{\text{other}}}$$

A variety from a r'_{yield} data is the ratio of the yield of that variety to the national yield per unit area, representing a high potential for a single variety.

$$r'_{\text{yield}} = \frac{\bar{y}_{\text{variety}}}{\bar{y}_{\text{national}}}$$

r_{area} and r_{yield} indicators are important measures of crop cultivation, with the former reflecting the diversity of planting structures and the latter reflecting the stability and improvement of variety yields.

Yield gap is defined as the difference between the average yield of the top five varieties (\bar{y}_{Top5}) and the unit area yield (Y_{mean}).

$$\text{yield gap} = \bar{y}_{\text{Top5}} - Y_{\text{mean}}$$

Building different types of models

A multiple linear regression model of the *yield rate*, r_{area} and r_{yield} was established using the `lm()` function in R software. The purpose of this model is to investigate the relationships between the *yield rate*, r_{area} and r_{yield} to determine how they contribute to crop yield. The model can be expressed as:

$$\text{yield rate} \sim r_{\text{area}} + r_{\text{yield}}$$

A multiple linear regression model for the *yield gap*, r_{area} and r_{yield} can be established using the `lm()` function in R.

$$\text{yield gap} \sim r_{\text{area}} + r_{\text{yield}}$$

A multiple linear regression model that improves upon the yield gap model can be created by adding an interaction term between r_{area} and r_{yield} . In this model, the `lm()` function in R is used to establish a multiple linear regression model with *yield gap* as the dependent variable and r_{area} , r_{yield} , and the interaction term between r_{area} and r_{yield} as the independent variables. The purpose of the model is to explore the interaction effects between different independent variables on the dependent variable.

$$\text{yield gap} \sim r_{\text{yield}} + r_{\text{area}} + r_{\text{yield}} : r_{\text{area}}$$

A multiple linear regression model was used to investigate the impact of the interaction between r_{area} and r_{yield} on *yield gap*. The R software's `lm()` function was used to establish a multiple linear regression model based on the *yield gap* and the interaction between different types of r_{area} and r_{yield} . This modeling approach can help clarify the impact of different types of r_{area} and r_{yield} on *yield gap*.

$$\text{yield gap} \sim \text{ind.}_{r_{\text{yield}}} : \text{ind.}_{r_{\text{area}}} + \text{jap.}_{r_{\text{yield}}} : \text{jap.}_{r_{\text{area}}}$$

Here, *jap.* represents *japonica*, *ind.* represents *indica*.

p value is used to verify whether the regression coefficient is significant. Adjusted R^2 is used to represent the fit of the model, n is the sample size, and k is the number of independent variables in the model, which is 2 in this model.

$$\text{adjusted } R^2 = 1 - (1 - R^2) \times \left(\frac{n-1}{n-1-k} \right)$$

Results

This study introduces a theory describing the interplay between planting area and crop yield enhancement. In this model, the control Variety C is used as the baseline, with its yield considered as the reference point. Although Variety A has a yield 40% higher than that of control Variety C, its limited adaptability results in a smaller planting area (i.e., only 10% of the total area nationally, with the remaining 90% occupied by Variety C) and, thus, a comparatively small contribution to national yield (4%; Fig. 1a). In contrast, although the yield of Variety B is only 20% higher than that of control Variety C, its wide adaptability allows a larger planting area (25% of the total planting area), resulting in a significantly higher yield contribution (5%; Fig. 1a). Thus, despite its lower yield, Variety B can make a greater contribution than Variety A to the national yield per unit area. We refer to this concept as the 'planting area–enhanced production theory'.

To validate the accuracy and universality of this theory, we analyzed a comprehensive dataset of Chinese national statistics for rice, maize, soybean, and wheat collected over a 30-year period. We investigated three key parameters (see Methods):

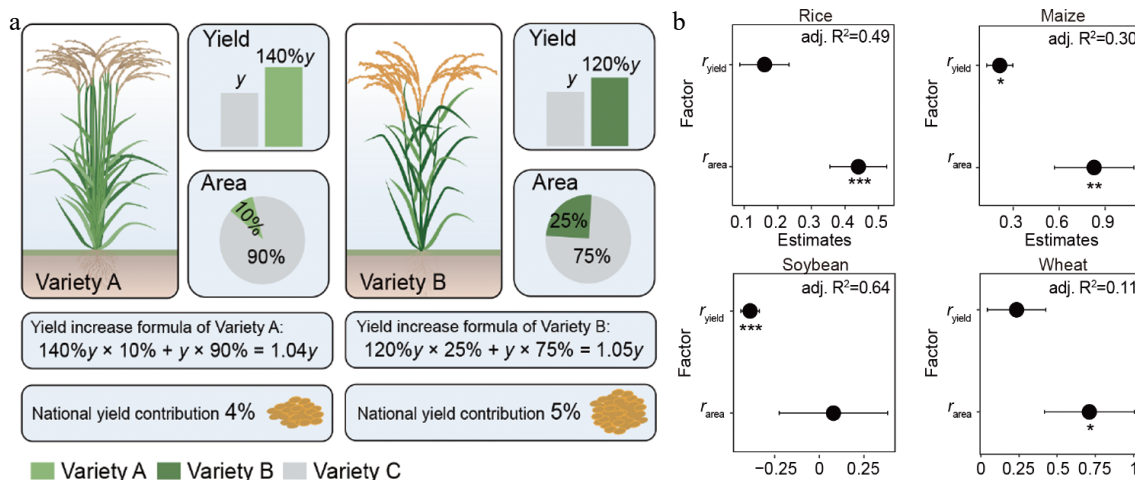


Fig. 1 Planting area–enhanced production theory. (a) Diagram illustrating the theory. y is the average yield of control Variety C. The rice plant as 'Created with BioRender.com'. (b) Multilevel linear regression for *yield rate* by r_{yield} to r_{area} in global regions. The 95% confidence intervals (CIs) of the partial regression coefficient are shown. The asterisk is used to represent the significance of the regression coefficient. (***) $p < 0.001$; $0.001 < ** p < 0.01$; $0.01 < * p < 0.05$

yield rate (the increase in yield per unit area); r_{yield} (the ratio of the highest yield to the average yield of a particular crop, which is used to measure the performance of a crop variety and to compare it with that of other crops); and r_{area} (the ratio between the maximum planting area occupied by a single variety and the total planted area). A high r_{yield} number indicates that a variety has a high potential for high yield compared to the average yield of the same crop. The r_{area} is an important indicator for evaluating the market share and geographic distribution of crop varieties. A high r_{area} value indicates that a variety is widely grown and occupies a large portion of the total cultivated area, while a low r_{area} value may suggest a less popular or available variety. Our findings reveal a weak positive correlation between the r_{area} and *yield rate* across different crop species, but we did not observe a consistent positive correlation between r_{yield} and *yield rate* across all crops (Supplemental Fig. S1). Additionally, our multiple regression analysis indicated that r_{area} has a significant positive impact on *yield rate* (Fig. 1b, Supplemental Table S1). These results support the theory that an increase in the planting area of specific crop varieties can lead to a substantial improvement in national yield, thereby confirming the validity and generalizability of the planting area–improved production theory.

The difficulties of bridging the yield gap under the limitations of social, biological, cultural, environmental, and abiotic constraints need close examination^[13,16,17]. There is currently a large yield gap in Southeast Asia, which limits its potential to continue to be a major global 'rice bowl'^[18]. Increased crop yields may be achievable by optimizing plant varieties and agricultural management strategies (nutrient availability, water management, etc.)^[12,19]. However, these strategies may conflict with national/economic human development needs and entail additional input, labour, and equipment costs. Therefore, understanding which traits of a crop variety can best contribute to narrowing the current yield gap will provide another tool to increase production and farm incomes. Our analysis delves more deeply into the potential contribution of the planting area–improved production theory not just to enhance yield per unit area but also, more broadly, to close yield gaps at the

national scale (Fig. 2a). We analyzed, at a national scale, the maximum yield ($\overline{y_{\text{Top5}}}$) as the approximately maximum genetic yield and the average yield per unit area (Y_{mean}) per annum of several crop varieties (rice, maize, soybean, and maize) to assess their yield gaps, defined as the difference between $\overline{y_{\text{Top5}}}$ and Y_{mean} . We found that the yield gaps in each species fluctuate over time (Fig. 2b). Furthermore, our results demonstrate significant positive correlation between r_{yield} and yield gap in rice, soybean, and maize (Supplemental Fig. S2a). Therefore, enhancing the maximum yield of a given crop variety may not improve the national average yield per unit area if that variety lacks adaptability, thus increasing the yield gap. Interestingly, only in rice did the r_{area} and yield gap show a strong negative correlation (Supplemental Fig. S2b). Furthermore, multiple regression analysis confirmed that the r_{area} exerted a robust negative effect on the yield gap in rice (Fig. 2c, Supplemental Table S2). These results suggest that high- r_{area} rice varieties contribute to improving the average yield per unit area and reducing the yield gap nationally (Fig. 2a).

Historical data from 1985 to 2016 show that high- r_{area} rice varieties were mainly planted before 2000 (Fig. 3a). Notably, from 1985 to 2000, high- r_{area} rice varieties were also the highest-yielding varieties (Fig. 3a), with Shanyou63 showing the highest r_{area} and yield (Fig. 4). No similar trend was observed in maize, soybean, or wheat (Fig. 3c, d). Nevertheless, maize and wheat showed rapid yield increases in periods when the r_{area} value was high, meaning that having one or a few varieties that were widely planted improved the national yield even when these varieties were not the highest-yielding ones available (Figs 1b, 3b–d, & 4). These results provide hard evidence for the theory we proposed (Fig. 1a). Multiple regression analysis further confirmed that the interaction between the r_{area} and r_{yield} significantly decreased the production gap in rice (Supplemental Fig. S3, Supplemental Table S3).

Our data indicated a shift in rice planting trend over time. Before 2000, the extensively planted high-yielding variety was Shanyou63. However, with the development of breeding techniques, a large number of high-yielding varieties have been bred. Since 2000, the predominant trend has been the planting

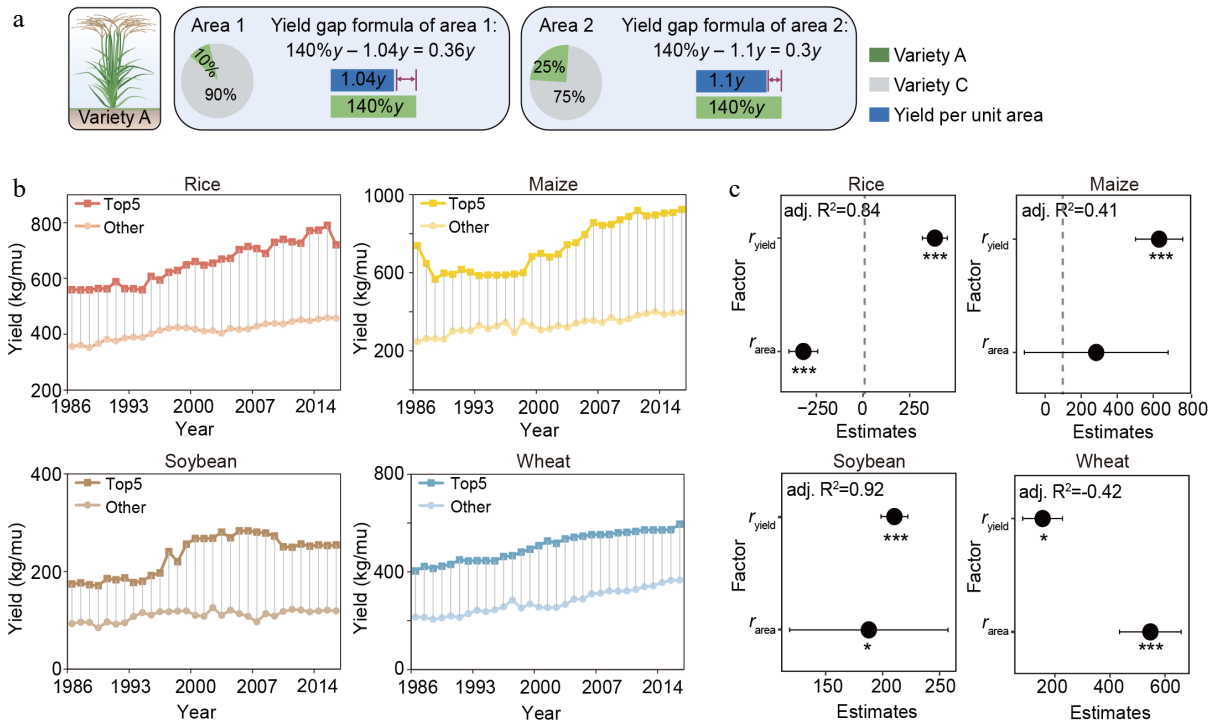


Fig. 2 Expanding the planting area helps reduce the yield gap in rice. (a) Modeling results showing the effect of large-scale planting of high-yielding varieties on the yield gap. y is the average yield of control Variety C. The rice plant as 'Created with BioRender.com'. (b) Yield gaps in different crops. (c) Multilevel linear regression for yield gap by r_{yield} to r_{area} of rice, maize, soybean, and wheat in global regions. The 95% confidence intervals (CIs) of the partial regression coefficient are shown. The asterisk is used to represent the significance of the regression coefficient. (***) $p < 0.001$; $0.001 < ** p < 0.01$; $0.01 < * p < 0.05$.

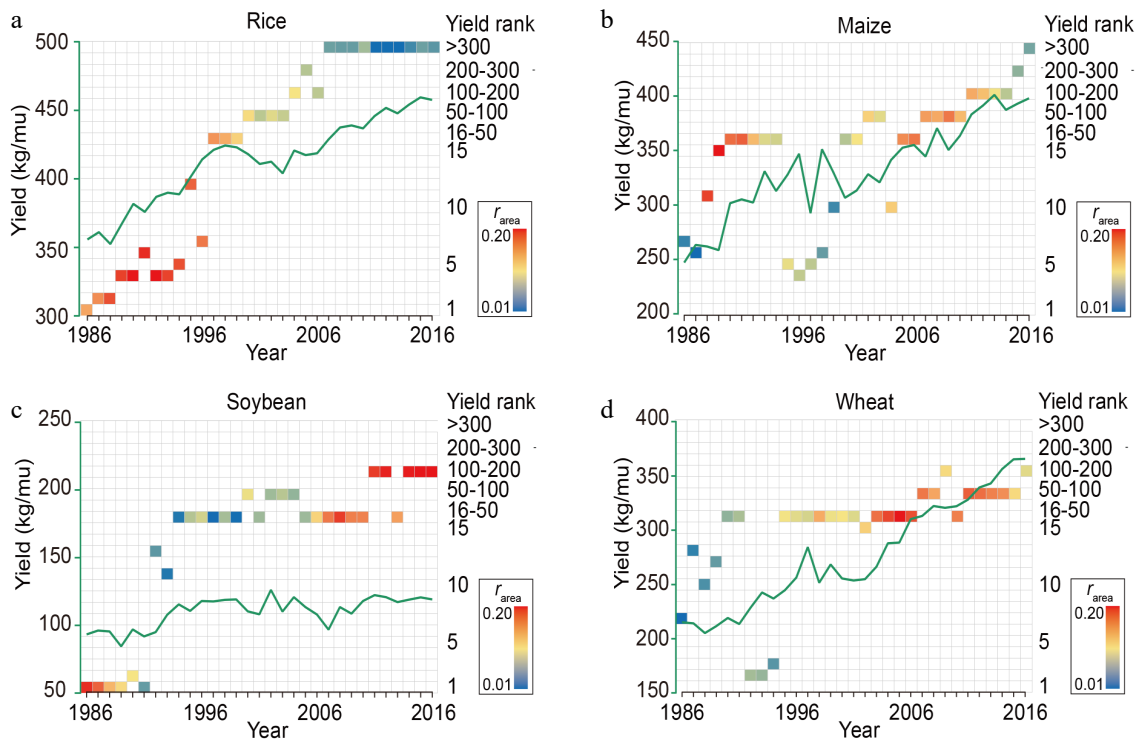


Fig. 3 r_{area} and yield ranking of the varieties with the largest planting area and yield per unit area for (a) rice, (b) maize, (c) soybean, and (d) wheat in different global regions. Each square represents a region, with colors representing the r_{area} and positions representing the yield ranking; the green lines represent the mean country yield per unit area planted.

of local high-yielding varieties in local conditions (Fig. 4). We divided the rice cultivation data into two cultivation intervals: 1986–2000 and 2001–2016, according to the planting trends. And we analyze the impact of r_{area} and r_{yield} on *yield rate*. Our results showed that r_{area} had a significant positive effect on *yield rate* during 1986–2000 (Supplemental Fig. S4a, b), indicating that the increase of rice yield in 2000 was mainly due to the

widespread planting of Shanyou63 (Supplemental Table S4). During 2001–2016, r_{yield} had a positive effect on *yield rate* (Supplemental Fig. S4c). However, when r_{area} was taken into account, r_{yield} no longer had a statistically significant effect on *yield rate* (Supplemental Fig. S4d). Despite the rise in rice production since 2000 (Fig. 3a), it is possible that other factors, such as industrial fertilizers and advancements in farming tech-

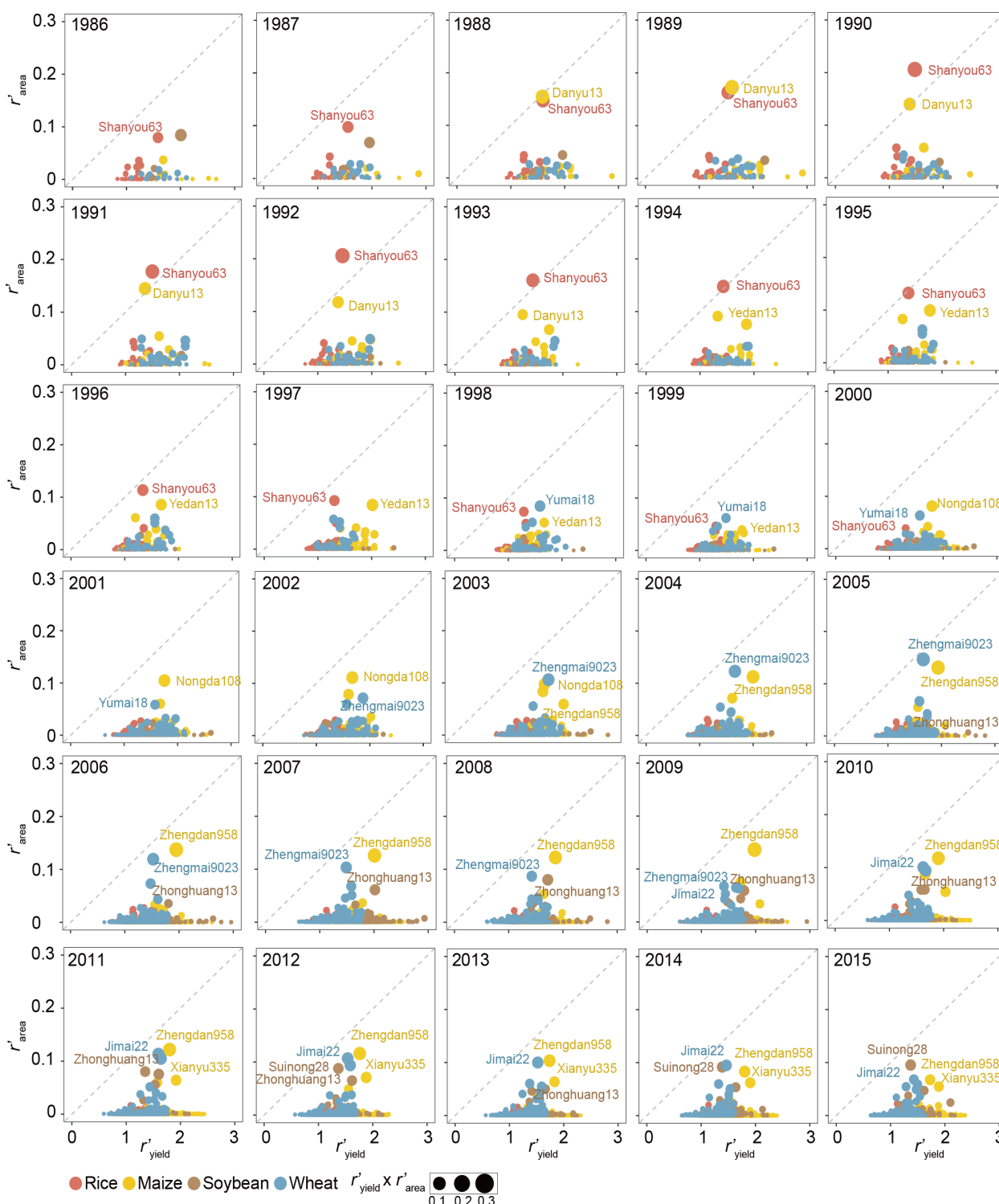


Fig. 4 r_{area} and r_{yield} of varieties in different crop. Circle color represents different crops, and circle size represents the value of $r_{area} \times r_{yield}$.

niques, attributable to the increase in yield. Furthermore, planting various high-yielding varieties according to local conditions necessitates a substantial allocation of germplasm resources. Consequently, we conclude that although planting high-yield varieties that adapt to local conditions can increase yield, the benefits are not as significant as those obtained through widespread planting the wide adaptation varieties (Supplemental Fig. S4e).

The planting area of *indica* rice was much larger than that for *japonica* rice in China, and Shanyou63 is an *indica* rice variety. So, when we assessed *japonica* and *indica* rice varieties separately, we found that the interaction between r_{area} and r_{yield} in *indica* rice significantly reduced the production gap, but this was not true for *japonica* (Fig. 5, Supplemental Table S3). Thus, extensive cultivation of the high-yielding *indica* variety Shanyou63 significantly increased the national average yield in 1985–2000. These findings support the idea that applying the planting area–improved production theory to high-yield, widely adaptable varieties can effectively reduce the yield gap (Fig. 2a).

IR8 ('miracle rice'), a representative Green Revolution rice variety, increased total rice yield from 60–150 to 250–350 kg/mu^[20] and was grown in more than 30 low-latitude countries and regions^[20] (Supplemental Fig. S5), perfectly conforming to the planting area–improved production theory. However, due to the mismatch between IR8's growth period and the cropping season in mid-latitude regions^[21], it is limited to low-latitude regions. Meanwhile, the high-yielding hybrid rice variety Shanyou63, with gradual daylength sensing coupled with optimized cropping systems to achieve multiple-latitude adaptation^[15], again demonstrated the validity of the planting area–improved production theory (Supplemental Fig. S5). Thus, outcomes from both the rice Green Revolution and hybrid rice breeding conform to our planting area–improved production theory, demonstrating the importance of plant broad adaptation for global food security.

Discussion

In China, annual soybean imports are ~90 million tons and are expected to exceed 100 million tons in 2023 (Supplemental

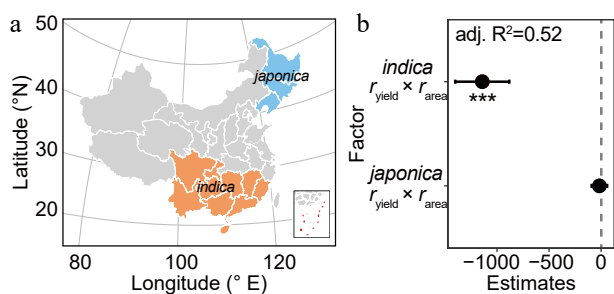


Fig. 5 The planting of *indica* rice helps reduce the yield gap. (a) Distribution of *indica* and *japonica* rice cultivars; provinces where both *indica* and *japonica* varieties were grown are omitted. (b) Multilevel linear regression for *yield gap* by interactions of r_{area} and r_{yield} in different rice ecotypes. *jap.* and *ind.* represent areas where *japonica* and *indica* cultivars are grown, respectively. The 95% confidence intervals (CIs) of the partial regression coefficient are shown. The asterisk is used to represent the significance of the regression coefficient. (***) $p < 0.001$; $0.001 < ** p < 0.01$; $0.01 < * p < 0.05$.

Fig. S6a). Only 250 million mu of land in China is suitable for soybean cultivation (Supplemental Fig. S6a), while 1 billion mu of arable land is needed to achieve self-sufficiency in soybean production. Heavy dependence on soybean imports contributes to the instability of global food security. Competition between rice, maize and soybean for arable land utilization is significant (Supplemental Fig. S6b), as a continuous increase in rice production is crucial for the efficient use of China's limited arable lands. Since 2000, the highest yield per mu of rice varieties in China has surpassed 800 kg/mu, but the national average yield remains 400 kg/mu (Fig. 2b). This may be due primarily to the poor adaptability of these high-yielding varieties, which limits their widespread planting (Figs 3a & 4), precluding application of the planting area–improved production theory to narrow the yield gap. Moreover, yield gaps are much higher for double-cropping than for single-cropping rice varieties^[22]. If narrowing the yield gap of double-cropping rice or modern high-yielding rice varieties can increase their proportion of total planting area, total rice yield can be secured with less cultivated land, and the surplus land can be used to alleviate the shortage of arable land for soybeans.

The emergence and advancement of agriculture have been significantly influenced by plant introductions and domestication. Therefore, in the process of seed introduction, it is imperative not only to select suitable seed materials but also to comprehensively understand the key ecological factors. Varieties with wide adaptability can be distributed over a wide range, so wide adaptation plays a crucial role in the seed introduction. The establishment of wide adaptation is based on multiple factors (e.g., daylength, disease resistance, cold tolerance, heat tolerance, etc.). Wide adaptation encompasses latitude adaptation, and the latter is a crucial aspect of achieving a comprehensive adaptation of varieties. Latitude adaptation presents significant challenges due to substantial variations in light, temperature, humidity, and pathogen microspecies at various latitudes. Achieving latitude adaptation requires coordination of multiple conditions to overcome these challenges. Our previous study suggests that daylength sensing is the key determinant of the latitudinal distribution of crops^[23]. Rice varieties with critical daylength sensing are suited for cultivation in low-latitude regions with relatively stable daylength, while daylength-insensitive rice thrives in high-latitude areas characterized by significant daylength fluctuations. Rice varieties that exhibit a gradual daylength sensing, in turn, possess greater flowering plasticity and can adapt to a wider range of growing regions. Therefore, relying on daylength sensing process can provide a foundational framework for breeding wide adaptation varieties. However, given the disparities in environmental factors beyond daylength among different regions, breeding efforts within the daylength perception framework also necessitate the consideration of comprehensive factors such as temperature sensitivity and resistance. Given that widespread promotion of a single variety can render crops susceptible to risks such as pests and diseases, and historical data show that the proportion of the planting area occupied by rice varieties resistant to rice blast fungus is higher than that occupied by blast-susceptible varieties (Supplemental Fig. S7), indicating that crop resistance traits can promote wide adaptability. So, breeding crops with broad resistance can help counter the risks of planting large areas of a single variety. Rice varieties adapted to high-latitude regions require not only daylength insensitivity

Planting area–enhanced production theory

but also cold tolerance. Conversely, rice varieties suited for low-latitude regions, in addition to their critical daylength sensing, should also exhibit heat tolerance.

Thus, using daylength sensing process as a fundamental framework, coupled with traits like temperature sensitivity and resistance, will be essential for breeding wide adaptation varieties in the future.

Improving the adaptability of high-yielding varieties will help expand their planting area, thereby increasing the overall national grain output. How to strengthen the adaptation of a high-yielding variety is the key point of perfecting this theory. In our previous research, we demonstrated that daylength sensing is a crucial factor influencing the latitude adaptation of crops, and varieties with gradual daylength sensing have the potential for multi-latitude adaptation^[15]. In addition, optimizing cropping modes can improve the multi-latitude adaptation of crops^[15]. Therefore, selecting high-yielding varieties with gradual daylength sensing and establishing their multi-latitude adaptation through cropping modes optimization is an important way to strengthen the adaptation of a high yielding variety. On the one hand, we can modify current varieties' photoperiodic genes to change their daylength sensing mode into gradual daylength sensing, but it's time-consuming. On the other hand, we also can use current varieties to establish a new cropping mode when the growth period of various crops can be rapidly predicted. Our results suggest that resistance to rice blast further enhances varietal risk tolerance and thus promotes crop wide adaptation. These results indicate that enhancing plant resistance, optimizing daylength sensing, and improving the cropping system can strengthen the adaptation of high-yielding varieties.

Conclusions

The mathematical principles behind the planting area–improved production theory are simple (Fig. 1a). However, in the absence of supporting data, people have grasped the importance of wide adaptability only intuitively. Our work now confirms this using historical data, providing a solid basis for incorporating wide adaptability as a breeding goal in genetic resource innovation and supporting rational allocation of crop planting areas at the national level. Currently, crop yield gaps in China (Fig. 2b), Europe, West Africa, and Southeast Asia significantly affect crop yield efficiencies^[12,13,18,24]. Our research suggests that promoting high-yielding, broadly adaptable varieties in these countries can help reduce yield gaps and alleviate global food security risks.

Author contributions

The authors confirm contribution to the paper as follows: research conception and design: Ouyang X; research performing: Wang X, Huang H, Lu M, Cui Y, Huang R, Wang X, Fu R, Liang W, and Ouyang X; data analysis: Wang X, Huang H, Liang W, and Ouyang X; draft manuscript: Wang X, Ouyang X. All authors reviewed the results and approved the final version of the manuscript.

Data availability

All data supporting the findings of this study are available within the paper and within its supplementary data published

online. Correspondence and requests for materials should be addressed to Ouyang X.

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Conflict of interest

The authors declare that they have no conflict of interest.

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