Perennial rice improves farmer livelihood and ecosystem security

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Abstract

To tackle food insecurity faced by an ever-growing population, there is an urgent need to develop new forms of highly productive and ecologically-secure agricultural systems. Crop perennialization provides a novel and promising solution to both food security and environmental challenges. Compared with annual grain production systems, which often undermine basic ecosystem services, perennial crops could maintain important ecosystem functions and reduce agricultural inputs. Here, we report our successful breeding of perennial rice (PR) taking over 20 years. We introduced perennial growth into domesticated Asian rice by interspecific hybridization and subsequently developed several perennial cultivars that have been commercialized recently in China and successfully trialed in multiple countries. The perennial cultivars produce yields comparable to commercialized annual rice (AR) varieties and maintain them for 4-5 consecutive years from a single planting. They exhibit robust regrowth, acceptable grain and milling quality, and are strongly preferred by farmers. We also quantified the social-economic, ecological and soil benefits attributable to perennial rice cultivation. Finally, we estimated the geographical areas potentially suitable for perennial rice cultivation worldwide, based on the correlation between regrowth rate and over-winter temperatures. Our innovation would help maintain food security and ecological integrity, and also inspire research on other perennial grains.

Background

Our human ancestors shifted from a diet derived entirely from hunting and gathering to one primarily reliant on farming annual grain crops that were domesticated either directly or indirectly from wild perennial progenitors. This ‘one-sow, one-harvest’ system underpinned the origin of human civilizations and continues to serve this function for today’s societies. Annual grains were domesticated independently on multiple continents since the beginning of the Neolithic revolution, and currently have become dominant crops that are grown on 60-80% of global croplands supplying 80% of global food [1, 2]. However, annual crops have some intrinsic disadvantages. They are often grown in industrialized monocultures that require high inputs of labour, energy, pesticides, and fertilizers [3]. This high-production input often compromises essential ecosystem services, pushing some beyond sustainable planetary boundaries [4-6]. Additionally, annual cropping systems typically provide only intermittent coverage of the soil by plants, leaving the barren soil vulnerable to heavy rainfall leaching or runoff, which carries substantial quantities of soil and nutrients off the land, reducing its fertility and resulting in the eutrophication of downstream aquatic ecosystems [7-9]. This situation especially occurs on marginal lands, which currently support 50% of world population and are at risk of further degradation under annual cropping [10, 11].

Perennial crops have advantages over annual crops in maintaining important ecosystem functions. Perennial crops generally have a longer photosynthetic season, which increases yearly light interception and enhances productivity [12]. Deep rooting, in addition to permanent living cover, reduces the risk of soil erosion and nutrition loss in perennial cropping systems relative to annual ones [13]. Moreover, perennial crops often require less inputs of fertilizer, pesticide, herbicide and labour, and can produce both grains and forages in mixed crop-livestock systems [14-16]. By meeting the dual needs of food security and environmental sustainability, perennial cropping systems not only allow farmers to make a living but also benefit ecological systems, which in-turn can improve agricultural productivity over the long-term [17-19].

In 2010, a team of scientists from more than 10 countries collectively predicted that commercially viable perennial grains would be available for agricultural production and would profoundly revolutionize agriculture[17]. Targeting key grains and oilseeds, including wheat, sunflower, barley, sorghum, buckwheat and rice, international researchers from numerous countries are engaged in developing the perennial counterparts of these annual crops using two breeding strategies– de novo domestication [20-22] and the inter-specific hybridisation [23-24]. The grain Kernza® is a perennial that exemplifies *de novo* domestication of the wild species *Thinopyrum intermedium*, or intermediate wheatgrass [25]. The perennial rice reported here utilized inter-specific hybridization to achieve a perennialism. While the potential for perennial crops to impact upon social and environmental challenges in agriculture, compared to annual grains, relatively little is known about the breeding of perennial grains and the agronomics of growing them. Here we report on progress in breeding recently commercialized perennial rice cultivars, including their performance over regrowth cycles and locations, as well as evaluations of socioeconomic, ecological and soil benefits of perennial rice cultivation over 10 successive seasons. Finally, we examine the possible and optimal zones of sustainable perennial rice production, and summarize potential impacts and prospects of perennial rice on the research and breeding of perennial grains worldwide.

Breeding Perennial Rice Via Interspecific Hybridization Benefited From Large Population Sizes And Backcrossing

A successful interspecific hybridization between the annual domesticated Asian rice *Oryza sativa* ssp. *indica* 'RD23' (a cultivar from Thailand) (Figure 1a, Extended Figure 1 & Extended Figure 2a) and an accession of the undomesticated African perennial and rhizomatous *O. longistaminata* (from Nigeria) (Figure 1b & Extended Figure 2b) was achieved using embryo rescue technology in 1996 [24]. The F_1 plant (Extended Figure 2c) possessed strong rhizomes, partial pollen fertility and self-compatibility, which provided a landmark material for basic research on the genetics of rhizome biogenesis and development in rice, and paved the way for the hybridization breeding of perennial rice cultivars [24, 26]. An exceptional F_2 individual, code 36-1, was selected in 2007 for subsequent breeding due to its high pollen fertility and seed-setting rate (greater than 85% and 60%, respectively), and moderately strong rhizome production (Extended Figure 1 & Extended Figure 2d).

From wide crosses, it can be difficult to obtain breeding lines with target traits due to linkage drag and low frequency of desirable alleles from the undomesticated parent, therefore we observed a low frequency of F_2s that were perennial, rhizomatous and had good agronomic characteristics. Thus, we screened 7200 F_2s to identify rare individuals with the best combination of traits from both parents for further breeding. Starting from the exceptional F_2, 36-1, we conducted multiple rounds of selfing. In each generation, only one individual with short rhizomes and good pollen fertility was selected for further self-pollination, and the crown of the chosen individual was retained. Consequently, a ‘population’ with individuals representing successive generations F_1 to F_9 was constructed (Extended Figure 3 & Extended Table 1), from which rhizome- and yield-related traits were investigated in 2018. As the generations advanced, the agronomic traits gradually changed in the direction of cultivated rice. From F_1 to F_9, we observed a decrease of rhizome number per plant (from 17 to 4) and rhizome length (from 9.3 cm to 3.4 cm) (Extended Figure 3 a & b). Also, pollen fertility gradually increased, and plant height, tiller number, grain number per plant, seed-setting rate, panicle length and grain size (grain length, width and weight) improved to reach values similar to those of widely-accepted rice cultivars (Extended Figure 3c-i). These data collectively showed that the perennial rice lines we developed had agronomic traits resembling domesticated annual rice, yet retained from the perennial *O. longistaminata* parent the ability to regrow vigorously after harvest.

More than 20 candidate perennial rice lines derived from the selfing F_2 selection 36-1 were evaluated for agronomic traits and perenniality in two multi-year field trials from 2012-2017 (experiment 1 and experiment 2) at ten locations in Yunnan, China and Lao PDR. Genotype by environment analyses revealed that broad-sense heritabilities were high for most traits (Extended Table 2 & Extended Table 3), including yield (0.87 to 0.94) and regrowth rate (0.88 to 0.96), indicating that the selections performed stably throughout the region. An especially promising line, subsequently named Perennial Rice 23 (PR23) (Figure 1c-d), exhibited high and stable grain yields over years and good performance (Figure 1e-h) at most locations [27-29], and was initially released to farmers in 2018 (*https://www.ricedata.cn/variety/varis/618801.htm,* in Chinese), a key milestone in the commercialization of perennial grains via inter-specific hybridization. Through further selections, three additional perennial rice lines were successfully bred, including Perennial Rice 24 (PR24), Perennial Rice 25 (PR25, released as “Yunda25” in 2020, *https://www.ricedata.cn/variety/varis/623354.htm*) and Perennial Rice 101 (PR101) (Extended Figure 1). PR23, PR24 and PR25 have grain quality traits similar to the *Japonica* subspecies of *O. sativa*, presumably obtained from their *O. longistaminata* parent, whereas PR101 has grain quality similar to its *indica* parent.

In a second round of breeding, our strategy was to transfer perenniality into local elite *O. sativa* cultivars. A perennial breeding line, MP3-235 (renamed PRB3 later), with strong perenniality and short rhizomes, (but less desirably 2-meters in height, with strong seed shattering and low grain density) (Extended Figure 2e-f) was chosen to cross with an elite *indica* cultivar, Dianrui 449 (DR449). Backcrossing was performed with DR449 as the recurrent parent, followed by several generations of selfing. From this backcross breeding, a new perennial rice cultivar, Perennial Rice 107 (PR107, DR449/MP3-235//DR449) (Extended Figure 1 & Extended Figure 2g-h), with strong perenniality, high yield and good grain quality was released as ‘Yunda107’ in China in 2020 (https://www.ricedata.cn/variety/varis/623356.htm) and in Uganda in 2021 (NARORICE1(PR107), https://naro.go.ug/).

Taken together, these results illustrate that our breeding strategy, based on large population size, and strong selection for perenniality and pollen fertility in recombinant inbred lines derived from an F_2 or backcross population was effective.

Performance And Adoption

To evaluate the productivity of PR23 in farm-scale plots (1.0-13.0 ha), an experiment was initiated in 2016 (Experiment 3) at three locations in Yunnan Province, Mengzhe (MZ), Xinping (XP) and Menglian (ML), where rice is typically planted from seed twice each year. The grain yield of PR23 at MZ was 10.9, 8.7, 8.2, 8.1 and 5.3 Mg ha^{-1} in the First season (F) of each year, respectively, and 6.6, 6.4, 6.2, 6.0 and 3.1 Mg ha^{-1} in the Second cooler season (S) over five successive years (Figure 2 & Extended Table 5). These yields (averaging 6.9 Mg ha^{-1}) were comparable with those of local elite annual rice, Diantun502 (averaging 7.0 Mg ha^{-1}), in four successive years (eight successive seasons), but gradually declined in the ninth season (Extended Figure 4a). Similarly, PR23 produced higher grain yields (averaging 7.7 Mg ha^{-1}) than the elite annual rice (Yunhui290: averaging 7.1 Mg ha^{-1}) in 8 successive seasons over four years at ML (Extended Figure 4c). At XP, however, the regrowth crop in spring 2017 (the first regrowth season) was severely damaged by rice hoppers and rats, but gain yields of PR23 were able to recover in the two subsequent seasons (averaging 6.0 Mg ha^{-1}) and showed comparable performance with Wenfu6 (the elite annual rice in XP) (averaging 6.1 Mg ha^{-1}) in the first three seasons; in the following seasons the yield was consistently lower but stable (Extended Figure 4b). Thus, PR23 sustainably produced high yields (averaging 6.8 Mg ha^{-1}) in each of four consecutive years (eight seasons) without re-sowing that were comparable with yield from currently leading annual rice cultivars (averaging 6.7 Mg ha^{-1}) replanted each season (Figure 2d). Similarly, the more recently released cultivars, PR25 and PR107, produced high and stable yields for at least two years and four seasons from a single planting in 2018 at multiple locations, and these were comparable to yields of PR23 (Experiment 4; Extended figure 5 & 6, Extended Table 6).

The high and stable grain yields maintained over eight seasons for PR23 were associated with a high regrowth rate (above 75%) and stable agronomic traits (Extended Figure 4). We observed that although the regrowth rate showed a decreasing trend over 10 seasons, the panicle number m^{-2} and other grain yield traits were maintained (except the damage in XP) resulting in stable yield (Extended Figure 4). This indicates an ability of perennial rice to regrow and tiller, which can compensate for the minor decrease in plant stand that may occur in later regrowth cycles, resulting in the panicle number and grain yield of perennial rice remaining stable to year 4. In the fifth year (i.e., the 9th and 10th seasons), however, grain yield decreased significantly due to a significant decrease in regrowth rate (below 75%), panicle number and spikelet number per panicle (Extended Figure 4), indicating a potential target trait for improvement of PR to further enhance its economic longevity. Thus, the regrowth rate of 75% may be a criterion for sustainable production of perennial rice. As with sugarcane [30], these first cultivars of perennial rice may need to be re-sown after about 8 growth cycles.

Thus, the three recently released cultivars of perennial rice that we bred (PR23, PR25 and PR107) can produce, from a single planting, high yields over two to four consecutive years for each of four to 10 cycles of growth-harvest-regrowth (regrowth) on plants that closely resemble modern *O. sativa* cultivars (Figure 2, Extended Figure 4, 5 & 6, Extended Table 5 & 6), whereas *O. sativa* cultivars can typically be ratooned at most only once, and with a substantial yield-drop in the ratoon crop [31-33]. Therefore, these first cultivars of PR represent a step-change that makes ratooning an economically attractive option for irrigated production environments that are not limited in duration by cold weather or other adverse environmental conditions. Moreover, these PR cultivars, along with Kernza® [18], are among the first perennial grains to be commercialized. By the year 2020, PR23 has been grown over 8400 ha. And in 2020, it was cultivated commercially on more than 11000 smallholder farmers and on 3818 ha, primarily in China (Figure 2).

Social And Economic Benefits

The dominant and prevailing annual cropping system of rice is labour intensive and thus costly, requiring seeding, ploughing, transplanting, crop management and harvesting every season, that leads to low economic profitability [28-29] as well as serious soil erosion [34-35]. Additionally, there are non-labour costs that include seed, pesticides, herbicides and fertilizers etc. [22]. To compare the economics of annual rice and perennial rice production, we measured the costs and returns associated with each.

In the first season of our study, costs were similar between annual and perennial rice (Figure 3a & Extended Table 7), for both the labour (1926-2012 US$ ha^{-1}) and non-labour (515-787 US$ ha^{-1}), which accounted for 71.3-79.5% and 20.5-28.7% of total economic cost, respectively (Extended Figure 7a-f). However, in the regrowth seasons, because perennial rice does not require seedling, ploughing and transplanting to initiate each crop, it was found to have an economic savings from lower labour cost (1057-1206 US$ ha^{-1}) and non-labour cost (96-201 US$ ha^{-1}), saving 1177-1401 US$ ha^{-1} (46.8-51% cost of annual rice) per regrowth season (Figure 3b &Extended Figure 7a-f & Extended Table 7).

Moreover, in each regrowth season, perennial rice production could save approximately 68~77 labour days ha^{-1} compared to annual rice, dramatically reducing drudgery and making the management of the perennial rice production system much easier (Figure 3c). This is particularly important because in most countries rural labour forces have declined due to urbanization [36], and thus the application of perennial rice will undoubtedly relieve the work burden of rural farmers, especially women and children. Equally important is that the reduction in human labour requirements are accomplished without substitution by fossil fuel-based mechanized traction, an important consideration as society aims to reduce greenhouse gas emissions associated with agricultural production. During 2016-2020, the net economic benefits of perennial rice in regrowth seasons at MZ, XP and ML averaged 882, 109 and 1165 US$ ha^{-1} season^{-1} which were 57.3%, 17.4% and 161% more than elite annual rice, respectively (Extended Figure 7i & Extended Table 7). Thus, even in the case where yields of perennial rice were significantly lower than annual rice (e.g. XP), perennial rice always achieved greater economic return (Figure 4d &

Extended Figure 7i). Adoption of perennial rice would thus reduce farm labour costs, energy use and technological inputs that are required for yearly tillage in annual cropping systems, thereby providing more profits to farmers than annual rice.

Soil Benefits

With soil tillage only required for the initial crop in the cycle, and with less soil disturbance, perennial rice cropping was expected to provide soil benefits over annual cropping. Perennial rice cropping over four years resulted in increased soil organic carbon (SOC) and total nitrogen (TN) at a rate of 0.81 and 0.11 Mg ha^{-1} year^{-1} at 0-40 cm soil layer, respectively (Figure 3g-h & Extended Figure 8 & Extended Table 8). The decomposition of rice stubble and crop residue resulted in more SOC and TN in the field, especially in the top 0-10 cm of soil in the perennial rice cropping system, and the increment would be expected to increase further with more cycles of perennial rice cultivation (Extended Figure 8j). Our results are consistent with a previous report which examined changes from annual to perennial cropping [37]. We found that the C/N ratio declined in the topsoil over years in the perennial cropping system (Extended Figure 8l), which would stimulate the microbe community to decompose more organic matter and provide more nitrogen in the soil [38]. Under no-tillage, perennial rice loosened deep soil (Extended Figure 8b-c), improved soil aeration (Extended Figure 8d-f) and increased soil water (Extended Figure 8g-i) and nutrient holding capacity (Extended Figure 8j-l). Additionally, the soil pH gradually increased to 5.99 after four years of no-tillage perennial rice cultivation, which is within the optimal range 5.0-6.5 for rice production and is more suitable for absorption of soil nutrients (including phosphorus, copper, zinc, boron, etc.) and microorganism activity[38] (Figure 3e). Our results showed that the improved soil structure of perennial rice helped conserve and use soil water and nutrients more efficiently. Moreover, perennial rice may reduce soil erosion, and soil evaporation, especially from the transplanting to tillering stage.

Optimal Ecological Zoning

We investigated which environmental factors were most critical for the regrowth of perennial rice. Based on data from 12 locations in four Provinces (Yunnan, Jiangxi, Guizhou, Guangxi; Experiment 5), the regrowth rate of perennial rice had a significant quadratic correlation with monthly average temperature of January 2017 (Extended Figure 9 & Extended Table 10). When the mean temperature in January was above 13.5 °C, the regrowth rate was always above 75%, and perennial rice attained higher grain yield in the next regrowth year (i.e. high crop stands lead to high yields). Additionally, when perennial rice was subjected to 0°C and 4°C for five days or more, the regrowth rate significantly decreased (Extended Table 11). Based on these findings, average temperature of the coldest month (above 13.5°C) and duration of the average daily temperature lower than 4°C for fewer than 5 days were the two key climate constraints for perennial rice growth.

Among 25049 meteorological stations worldwide (National Centers for Environmental Information, https://www.ncei.noaa.gov/), 2659 meet these climate constraints and thus may be suitable for perennial rice, suggesting that perennial rice has a broad range of potential planting regions in the world (Figure 3d).

Conclusion And Prospects

After more than 20 years of effort, the cultivation of perennial rice has become a reality. This represents a novel cropping system that achieves both grain production, labour reduction and ecological security, especially for terraced and fragile farmland. Perennial rice has demonstrated good yield potential and agronomic traits for four years and eight cropping seasons from a single planting, and can simplify rice production, enhance soil fertility, and protect the environment. The simplified management, reduced labour requirements and increased economic returns offered by perennial rice are attractive to farmers (more than 11000 smallholder farmers in 2020), and this technology is currently becoming well-accepted by more and more farmers. Widespread adoption of perennial rice can reduce intensive tillage and soil erosion, and reliance on inputs. Successful cultivation of perennial rice, however, will require greater focus on ecological management of weeds, fertility and stubble. Our perennial rice has received certification for commercialization due to the multifaceted benefits it brings, providing an optimal solution that reconciles food production with environmental security and the needs of farmers.

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Figures

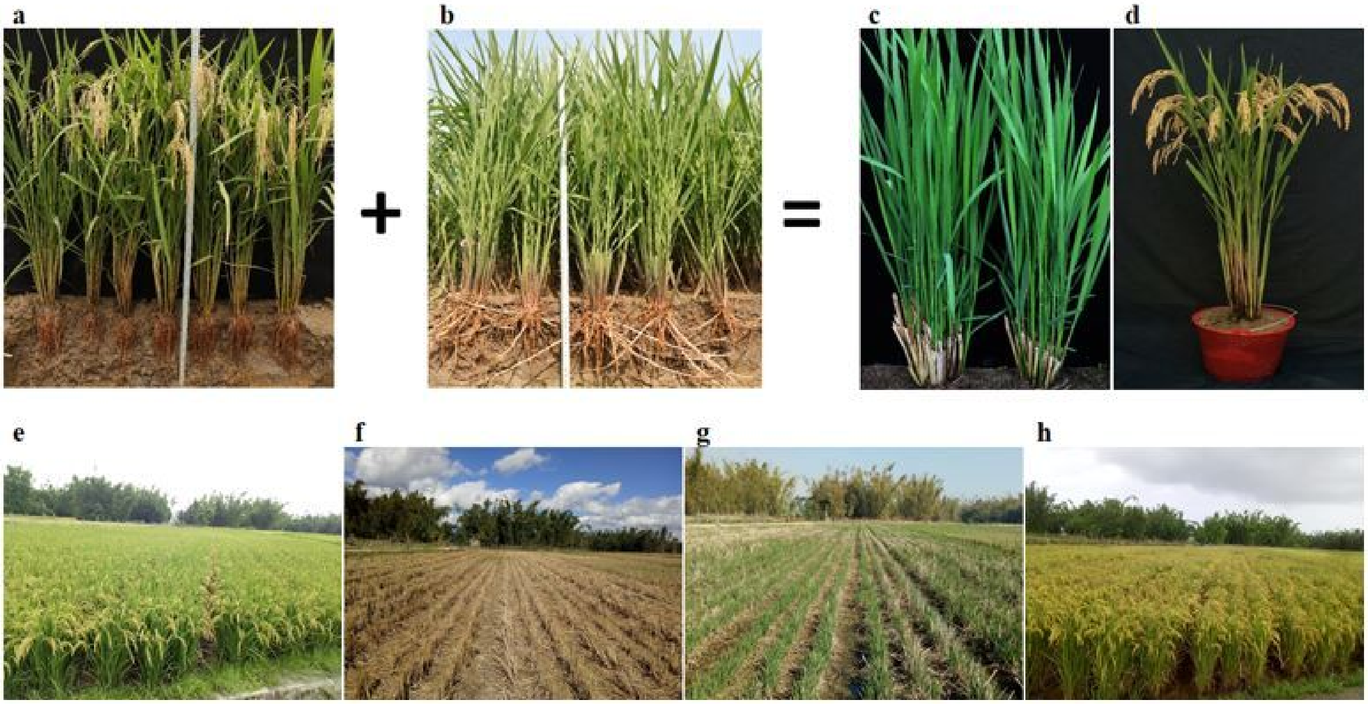

Figure 1

Innovation of perennial rice for sustainable production. a, RD23, *Oryza sativa*, annual rice as female parent. **b**, *O. longistaminata*, perennial rice with strong rhizomes as male parent. **c**, PR23, perennial rice selection showing excellent regrowth aboveground (note both the numerous new green shoots and the cut brown shoots from the previous season). **d**, PR23 at maturity after regrowth. **e-h**, performance of PR23 at Mengzhe, Yunnan, China (MZ, 21°57'N, 100°14'E, 1255 m). **e**, PR23 at maturity in the first year. **f**, PR23 overwinter in the first year. **g**, PR23 regrowth in the second year. **h**, PR23 at maturity in the second year (note strong plant stand and high yields).

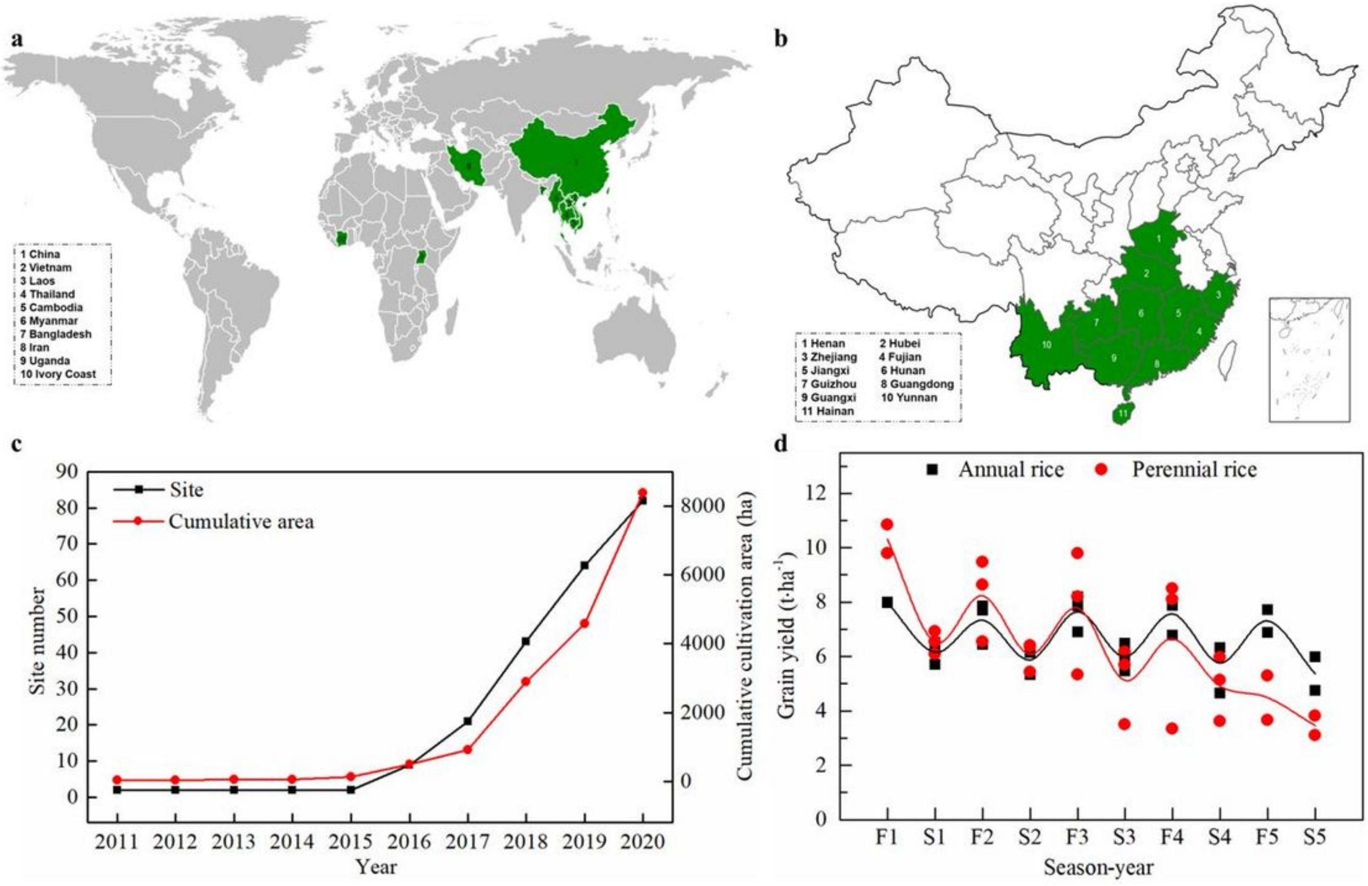

Figure 2

Cultivation of perennial rice in the world has expanded in geography and area since its introduction in 2011. a, Where perennial rice has been cultivated in the world. Perennial rice has been tested in more than 10 countries, including China, Vietnam, Laos, Thailand, Cambodia, Myanmar, Bangladesh, Iran, Uganda, Ivory Coast. **b**, Cultivation of perennial rice in China. Perennial rice has been tested in more than 10 provinces, including Henan, Hubei, Zhejiang, Fujian, Jiangxi, Hunan, Guizhou, Guangdong, Guangxi, Yunnan and Hainan. **c**, Number of production locations and cumulative area of perennial rice production in China since 2011. As PR017 and PR25 were released in 2020, the data of the cultivation area was mostly for PR23. **d**, Grain yield of perennial rice over five years with ten successive seasons between 2016 and 2020. F1 to F5 represent the first season of year 1 to year 5, S1 to S5 represent the second season of year 1 to year 5. The data of grain yield were derived from experiment 3, see Extended Tables 4 and 5 and Extended Figure 4.

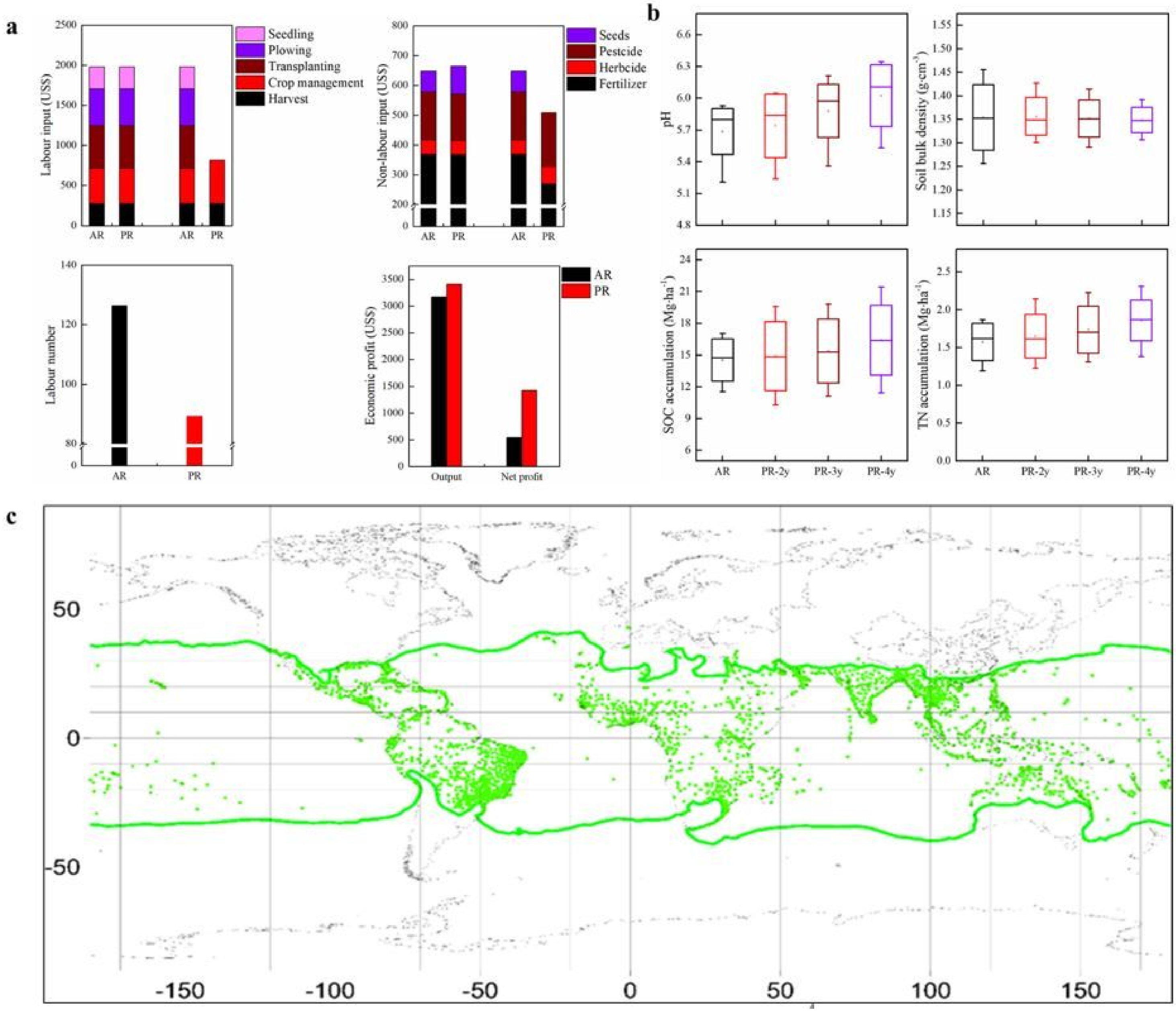

Figure 3

Social–economic benefits, environmental benefits and potential planting regions of perennial rice. a, social–economic benefit of perennial rice. In rice production, the economic cost including labour and non-labour cost. Labour cost mainly including seedling, plowing, transplanting, crop management, harvest, etc. Non-labour cost including seed, pesticide, herbicide, fertilizer, etc. The output refers to the gross income from grain sales. The net economic gain equals to the output minus total cost. For annual rice, seed, plowing, seedling, transplanting, crop management and harvest are all needed in each season. For perennial rice, seed, plowing, seedling, transplanting, crop management and harvest are all needed in the first season that was similar to annual rice; however, in the subsequent seasons, tillers of the plant are accomplished by regrowth, and thus seed, seedling, plowing and transplanting are not performed, resulting in considerable savings of money and labour. 1 US$ =6.4 China Yuan, the date for exchange was due to the rate of 4 Nov 2021. AR, annual rice. PR, perennial rice. The data derived from experiment 3, in Extended Table 7 and Extended Figure 7. **b**, Soil benefits of perennial rice cropping system. The soil properties refer to the depth of 0-40 cm soil layers. AR, annual rice. PR-2y, PR-3y and PR-4y are perennial rice year 2, perennial rice year 3 and perennial rice year 4, respectively. The data derived from experiment 3, in Extended Table 8 and Extended Figure 8. **c**, Optimal ecological zoning of perennial rice. The data derives from 25049 meteorology stations from 2015 to 2020 (6 years), obtained from the National Oceanic and Atmospheric Administration's (NOAA) National Centers for Environmental Information (NCEI) website (https://www.ncei.noaa.gov/). Based on our findings from experiment 5 in Extended Tables 10 and 11 and Extended Figure 9, we selected the regions suitable for planting perennial rice, in which the average monthly temperature was higher than 13.5 ℃ (contours), and in which the average daily temperature was lower than 4 ℃ lasted for fewer than five days (green dots within the contours; 2695 stations).

Supplementary Files

This is a list of supplementary files associated with this preprint. Click to download.

- extendedTables20220127.docx
- extendedfigures20220127.docx