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Sustained productivity and agronomic potential of perennial rice

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There is an urgent need for agricultural systems to intensify sustainably, increasing crop productivity, farmer livelihoods and soil health while using fewer resources. Crop perennialization, the conversion of especially annual grains to perennial forms, has shown such possibility. Here we report the successful breeding of perennial rice and assess its performance and potential. Domesticated, annual Asian rice (*Oryza sativa*) was hybridized with its perennial African relative *Oryza longistaminata*. From a single planting, irrigated perennial rice produced grain for eight consecutive harvests over four years, averaging 6.8 Mg ha^{-1} harvest^{-1} versus the 6.7 Mg of replanted annual rice, which required additional labour and seed. Four years of cropping with perennial rice resulted in soils accumulating 0.95 Mg ha^{-1} yr^{-1} organic carbon and 0.11 Mg ha^{-1} yr^{-1} nitrogen, along with increases in soil pH (0.3–0.4) and plant-available water capacity (7.2 mm). Perennial cultivars are strongly preferred by farmers; growing them saves 58.1% of labour and 49.2% of input costs in each regrowth cycle. In 2021, perennial rice was grown on 15,333 ha by 44,752 smallholder farmers in southern China. Suited to a broad range of frost-free environments between 40° N and 40° S, perennial rice is a step change with potential to improve livelihoods, enhance soil quality and inspire research on other perennial grains.

Our ancestors shifted from a diet derived entirely from hunting and gathering to one reliant primarily on farming annual grain crops that were domesticated either directly or indirectly from wild perennial progenitors[1,2]. This one-sow, one-harvest system underpinned the origins of civilizations and continues to feed today's societies[3]. Annual grains, domesticated independently on multiple continents from the beginning of the Neolithic revolution, are currently grown on 60–80% of global croplands, supplying 80% of global food[4,5]. However, modern high-yielding annual crops require wholesale removal of competing vegetation to establish and typically demand high inputs of energy, pesticides and fertilizers (and, in some cases, labour) to be productive[6]. The combination of chronic soil disturbance and high inputs often

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compromises essential ecosystem services, pushing many beyond sustainable planetary boundaries[7–9]. In addition, annual crops typically provide only intermittent coverage of the soil by plants, leaving barren soil vulnerable to heavy rainfall, which carries substantial quantities of soil and nutrients off the land, reducing its fertility and resulting in the eutrophication of downstream aquatic ecosystems[10–12]. This situation occurs especially on marginal lands, which currently support 50% of the world's population and are at risk of further degradation under annual cropping[13,14].

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[15]. In addition to permanent living cover, deep roots of perennial crops have been shown to increase nitrogen (N) retention[11,12]and soil carbon accumulation[16,17] and may ultimately require lower rates of fertilizer, pesticide and labour inputs[9]. Perennial cropping systems can also be managed to produce both grains and forages in mixed crop–livestock systems[5,18–21]. By improving labour efficiency and soil quality, perennial cropping systems not only improve farmers' livelihoods but also benefit the ecological systems required to maintain productivity over the long term[20–22].

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[23–25] and interspecific hybridization[26,27]. The grain Kernza® is a perennial that exemplifies *de novo* domestication of the wild species *Thinopyrum intermedium*, or intermediate wheatgrass[28]. The perennial rice (PR) reported here was developed by interspecific hybridization. It was targeted initially at favourable (irrigated) rice production systems, in which paddy fields are bunded and ponded water depth is carefully managed. Nevertheless, rice is cultivated across a wide range of ecosystems, from flood-prone to rainfed lowland and rainfed upland, in which submergence and drought define the crop's adaptive characteristics[29]. We report on progress in breeding recently commercialized PR cultivars, including their performance over regrowth cycles and locations, and evaluate the livelihood, ecological and soil benefits of PR cultivation over ten successive seasons. We then examine potential zones for sustainable PR production and consider the prospects, limitations and impacts of research, development, adoption and commercialization of this crop, and hence of perennial grains worldwide.

Breeding PR via interspecific hybridization

A successful interspecific hybridization between the annual domesticated Asian rice *Oryza sativa* ssp. *indica* RD23, a cultivar from Thailand (Fig. 1a and Extended Data Figs. 1 and 2a), and an accession of the undomesticated African perennial and rhizomatous *O. longistaminata* from Nigeria (Fig. 1b and Extended Data Fig. 2b) was achieved by embryo rescue in 1996[27]. The F_1 plant (Extended Data Fig. 2c) possessed strong rhizomes, partial pollen fertility and self-compatibility, which provided foundational material for basic research on the genetics of rhizome biogenesis and development in rice and paved the way for breeding PR cultivars[27,30].

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, were rhizomatous and had good agronomic characteristics. To circumvent this linkage drag, we used pedigree selection from the best single plant in each generation and screened 7,200 F_2s to identify rare individuals with the best combination of traits from both parents for further breeding. In 2007, an exceptional F_2 individual, coded 36–1, was selected due to its high pollen fertility and seed-setting rate (greater than 85% and 60%, respectively) and moderately strong rhizome production (Extended Data Figs. 1 and 2d).

Starting from the exceptional F_2 36–1, we conducted multiple rounds of self-pollination. In each generation, only one individual with short rhizomes and good pollen fertility was selected for self-pollination, and the crown of the chosen individual was retained. Consequently, we constructed a population with individuals representing successive generations from F_1 to F_9 (Extended Data Fig. 3 and Supplementary Table 1) and used this population to investigate rhizome- and yield-related traits 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 in rhizome number per plant (from 17 to 4) and rhizome length (from 9.3 cm to 3.4 cm) (Extended Data Fig. 3a,b). 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 planted annual rice (AR) cultivars (Extended Data Fig. 3c–i). These data collectively showed that the PR lines we developed had agronomic traits resembling domesticated AR yet retained from the perennial *O. longistaminata* parent the ability to regrow vigorously after harvest. From next-generation sequencing, 16.16% of the PR23 genome was *O. longistaminata*.

More than 20 candidate PR lines derived from self-pollinating the F_2 selection 36–1 were evaluated for agronomic traits and pereniality in two multi-year field trials from 2012 to 2017 at ten locations in Yunnan, China and Laos[31,32] (Experiments 1 and 2; Supplementary Tables 2 and 3). Genotype-by-environment analyses revealed that broad-sense heritability was high for most traits, including yield (0.87 to 0.94) and regrowth rate (0.88 to 0.96), indicating that the selections were stable throughout the region. An especially promising line, subsequently named PR 23 (PR23) (Fig. 1c,d), exhibited high and stable grain yields over multiple years and good performance (Fig. 1e–h) at most locations[33,34]. PR23 was released to farmers in China in 2018[35], a key milestone in the commercialization of perennial grains bred via interspecific hybridization. Through further selection, three additional PR lines were successfully bred: PR24, PR25 (released as Yunda25 in China in 2020[36]) and PR101 (Extended Data Fig. 1). PR101 has grain quality similar to its *O. sativa* ssp. *indica* parent RD23, which has a high grain length/width ratio of 3.57, whereas PR23, PR24 and PR25 have grain quality traits similar to the typical *O. sativa* ssp. *japonica* cultivar Zhonghua 11, including a lower grain length/width ratio of 2.13. These grain qualities should be widely accepted as they are similar to current consumer preferences, except in countries such as Tanzania, Ethiopia and Laos, which have specific grain quality requirements[37,38].

In a second round of breeding, our strategy was to transfer perenniality into local elite *O. sativa* cultivars. A perennial breeding line MP3–235 (later renamed PRB3), with strong perenniality and short rhizomes but (less desirably) a 2 m plant height, strong seed shattering and low grain density (Extended Data Fig. 2e,f), was chosen to cross with an elite *indica* cultivar, Dianrui 449 (DR449). Three generations of backcrossing (240 lines each) to DR449 as the recurrent parent were performed, followed by several generations of self-pollination. As expected, backcrossing to an elite parent increased the frequency of progenies with desirable agronomic traits relative to the F_2 population (Supplementary Table 1). From this backcross breeding, a new PR cultivar, PR107 (DR449/MP3–235//DR449) (Extended Data Figs. 1 and 2g,h), with strong perenniality, high yield and good grain quality, was released as Yunda107 in China in 2020[39] and as NARORICE-1 (PR107) in Uganda in 2021. 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

We initiated an experiment in 2016 to evaluate the productivity of PR23 in farm-scale plots of 1–13 ha (Experiment 3). This took place at three locations in Yunnan Province, Mengzhe, Menglian and Xinping, where rice is

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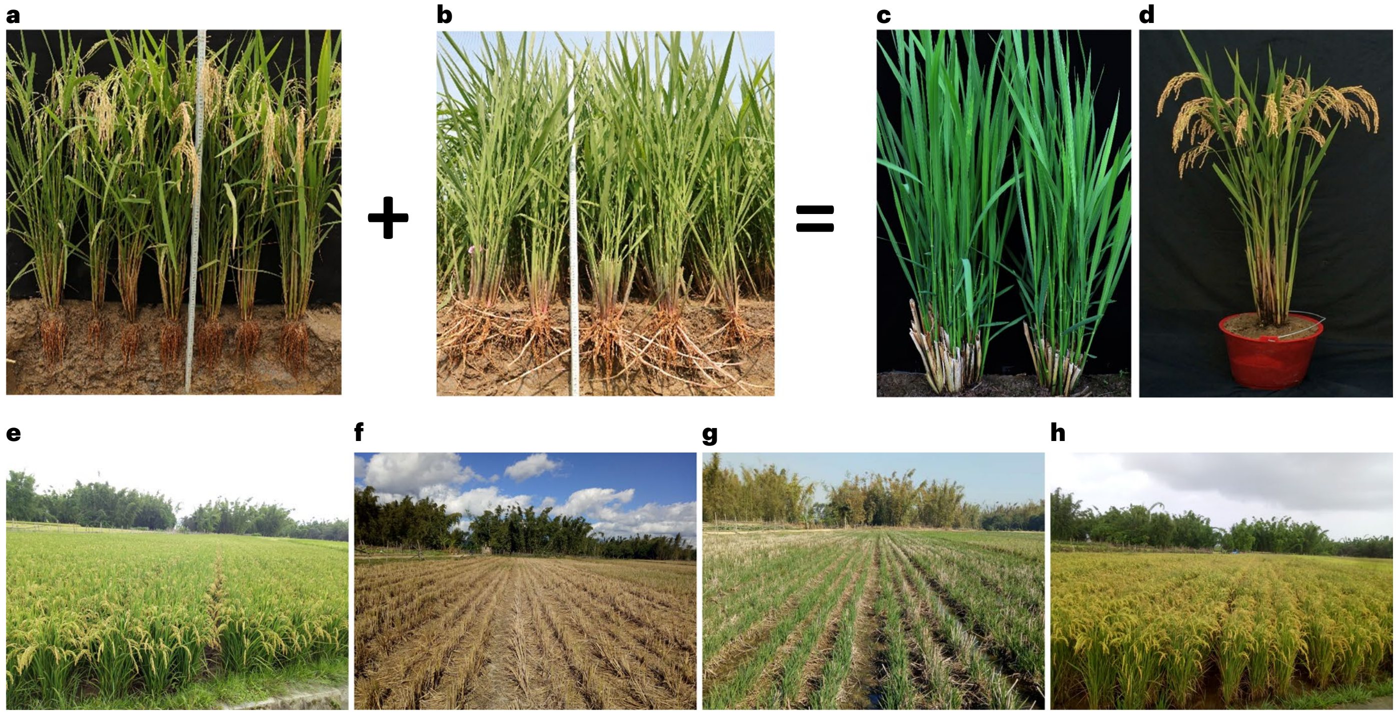

Fig. 1 | Innovation of PR for sustainable production. **a**, RD23, *Oryza sativa*, annual rice as female parent. **b**, *O. longistaminata*, perennial rice with strong rhizomes as male parent. **c**, PR23, perennial rice selection showing excellent regrowth above ground. Note both the numerous new green shoots and the cut brown shoots from the previous season. **d**, PR23 at maturity after regrowth. **e**–**h**, Performance of PR23 in Mengzhe, Yunnan, China (21° 57′ N, 100° 14′ E, 1,255 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 yield.

typically planted from seed twice a year. The grain yield of PR23 in Mengzhe over five successive years was 10.9, 8.7, 8.2, 8.1 and 5.3 Mg ha^{-1} in the first season of each year, respectively, and 6.6, 6.4, 6.2, 6.0 and 3.1 Mg ha^{-1} in the cooler second season (Fig. 2 and Supplementary Table 4). These yields (averaging 6.9 Mg ha^{-1}) were comparable to those of the local elite AR Diantun502 (averaging 7.0 Mg ha^{-1}) in eight successive seasons over four years but gradually declined in the ninth season (Extended Data Fig. 4a). Similarly, Menglian PR23 produced higher grain yields (averaging 7.7 Mg ha^{-1}) than the local elite AR Yunhui290 (averaging 7.1 Mg ha^{-1}) in eight successive seasons over four years (Extended Data Fig. 4c). In Xinping, the regrowth crop in spring 2017 (the first regrowth season) was severely damaged by rice hoppers and rats, but grain yields of PR23 were able to recover in the two subsequent seasons (averaging 6.0 Mg ha^{-1}) and showed performance comparable to the local elite AR Wenfu6 (averaging 6.1 Mg ha^{-1}) in the first three seasons; in the following seasons, the yield was consistently lower but stable (Extended Data Fig. 4b). Across the experiment, therefore, PR23 sustainably produced yields averaging 6.8 Mg ha^{-1} in each of four consecutive years (eight seasons) without re-sowing, and these were comparable to yields from the current leading AR cultivars, which averaged 6.7 Mg ha^{-1} after being replanted each season (Fig. 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 (Experiment 4), and these were comparable to yields of PR23 (Extended Data Figs. 5 and 6 and Supplementary Table 5). 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 Data Fig. 4), suggesting PR would need to be resown after about four years. Alternatively, PR could be rotated with a legume pasture or a pulse or brassica crop to provide a break from pests, diseases and weeds and to support other farm enterprises such as livestock while further improving soil health.

Removal of PR after eight harvests, pests, diseases and weeds pose potential threats to successful adoption, and these are considered in detail in Methods, together with strategies to reduce risks. Briefly, adoption of PR is not without risks to the farmer, as 1–2 more herbicide applications were required in PR ratoon cycles than in transplanted AR in our experiments (Supplementary Table 6). While not encountered in our experiments, pests and diseases adapted to high N applications could pose threats under irrigated conditions, especially if pustule loads in stubble are large or insect-transmitted viruses such as tungro become established in regenerating plant crowns. Short rhizomes were intentionally selected in PR so as not to provide substantial weed potential but to permit improved chances of survival and regrowth when harsher conditions were encountered. Under irrigation, therefore, tillage may be required to expose PR crowns to soil drying, perhaps with follow-up glyphosate spraying of young regrowth if needed before re-sowing. Further details are provided in Methods, including on our pest-, disease- and weed-control strategies.

In summary, the three recently released cultivars of PR 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 ten cycles of growth–harvest–regrowth on plants that closely resemble modern *O. sativa* cultivars (Fig. 2, Extended Data Figs. 4, 5 and 6 and Supplementary Tables 4 and 5), whereas *O. sativa* cultivars can typically be ratooned at most only once, and with a substantial yield drop in the ratoon crop[40–42]. 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. These cultivars, along with Kernza®[21], are also among the first perennial grains to be commercialized. By 2020, PR23 was being grown on over 8,400 ha. In 2020, it was cultivated commercially on 3,818 ha by more than 11,000 smallholder farms, primarily in China (Fig. 2c and

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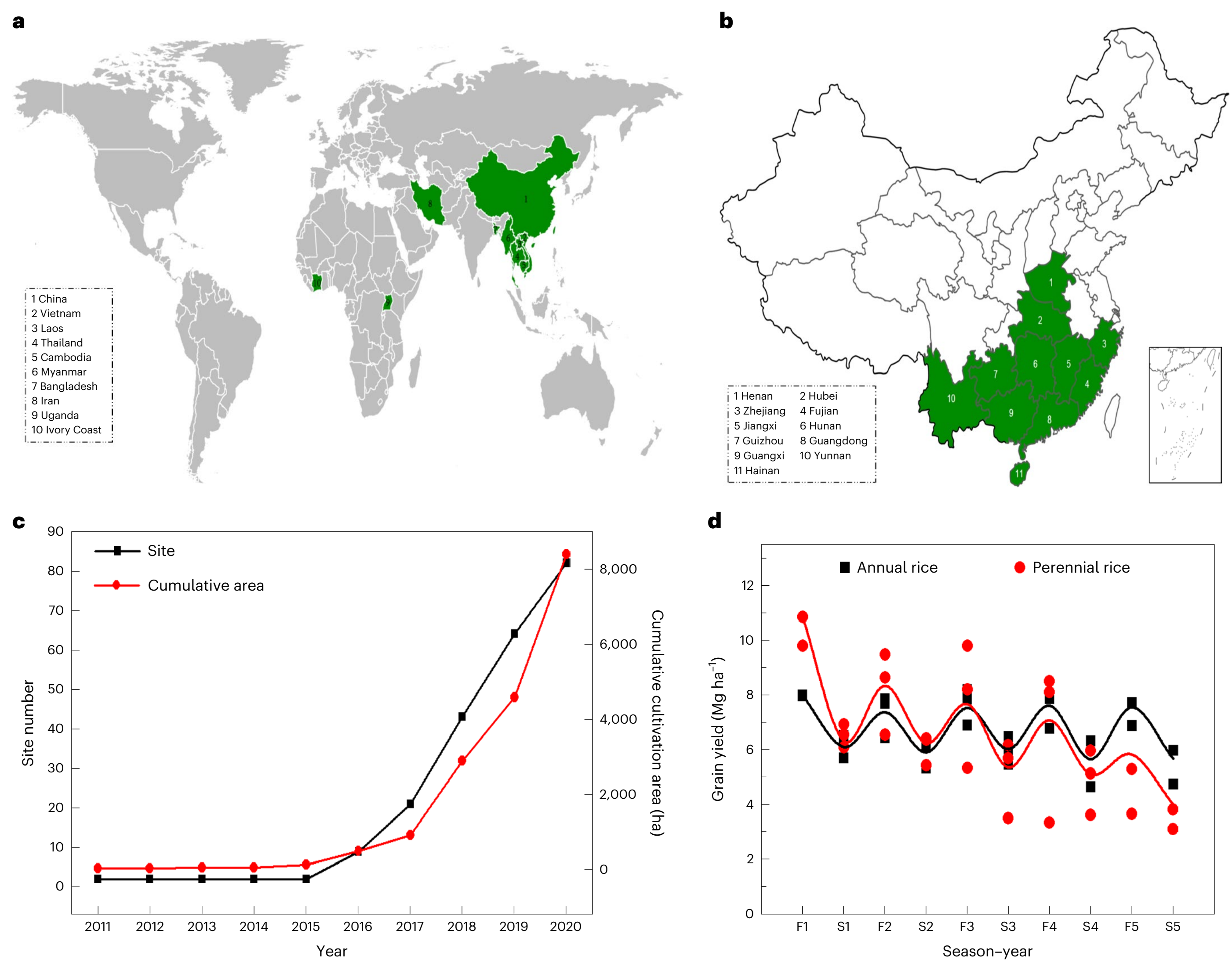

Fig. 2 | Cultivation of PR has expanded in geography and area since its introduction in 2011. a, Cultivation of PR globally. **b**, Cultivation of PR in China. **c**, Number of production locations and cumulative area of PR production in China since 2011. As PR107 and PR25 were released in 2020, the data for cultivation area are mostly for PR23. The least significant difference (LSD) for location and area were 5 and 4, derived from LSD for log(location) and log(area), respectively ($P < 0.05$) (Supplementary Table 7). **d**, Grain yield of PR23 over five years with ten successive seasons between 2016 and 2020. F1–F5 represent the first seasons of years 1–5; S1–S5 represent the second seasons of years 1–5. The LSD for grain yield was 1.7 Mg ha^{-1} ($P < 0.05$), with the data derived from Experiment 3 (Supplementary Table 4 and Extended Data Fig. 4).

Supplementary Table 7). In 2021, the planting area of PR increased to 15,533 ha, including 44,752 smallholder farms, demonstrating a rapid adoption of PR—a fourfold increase in area and number of farmers in one year.

Livelihood benefits

The prevailing irrigated annual cropping system of rice is labour intensive and thus costly, requiring seedling nurseries, ploughing, transplanting, crop management and harvesting every season. Non-labour costs also include seed, pesticides, herbicides and fertilizers. These expenses lead to low profitability[33,34] and insecure livelihoods. To compare the socioeconomics of annual and PR production, we measured the grain yields, labour requirements, inputs costs and returns associated with each. These data are summarized in Supplementary Table 8, which aggregated labour costs for seedling nurseries, ploughing, transplanting, crop management and harvesting. Note that fuel costs are included within ploughing, transplanting and harvesting; fertilizer costs are included within nurseries, ploughing, transplanting and crop management; and pesticide costs are included within ploughing and crop management. Under crop management, the additional cost of each regrowth cycle in Mengzhe and Menglian is for weed control ($74 ha^{-1} on average), and in Xinping the further $82 ha^{-1} is for pest control, as noted earlier.

In the first season of our study, costs were similar between annual and PR (Fig. 3a and Supplementary Table 8) for both the labour (US$1,926–2,012 ha^{-1}) and non-labour (US$515–787 ha^{-1}), which accounted for 71.3–79.5% and 20.5–28.7% of total economic cost, respectively (Extended Data Fig. 7a–f). However, in the regrowth seasons, because PR does not require seedling nurseries, ploughing or transplanting to initiate each crop, it was found to have economic savings from lower labour cost (US$1,057–1,206 ha^{-1}) and non-labour costs (US$96–201 ha^{-1}), saving US$1,177–1,401 ha^{-1} (46.8–51% of the costs of AR) per regrowth season (Fig. 3b, Extended Data Fig. 7a–f and Supplementary Table 8).

Moreover, in each regrowth season, PR production could save approximately 68–77 labour days ha^{-1} compared with AR, dramatically

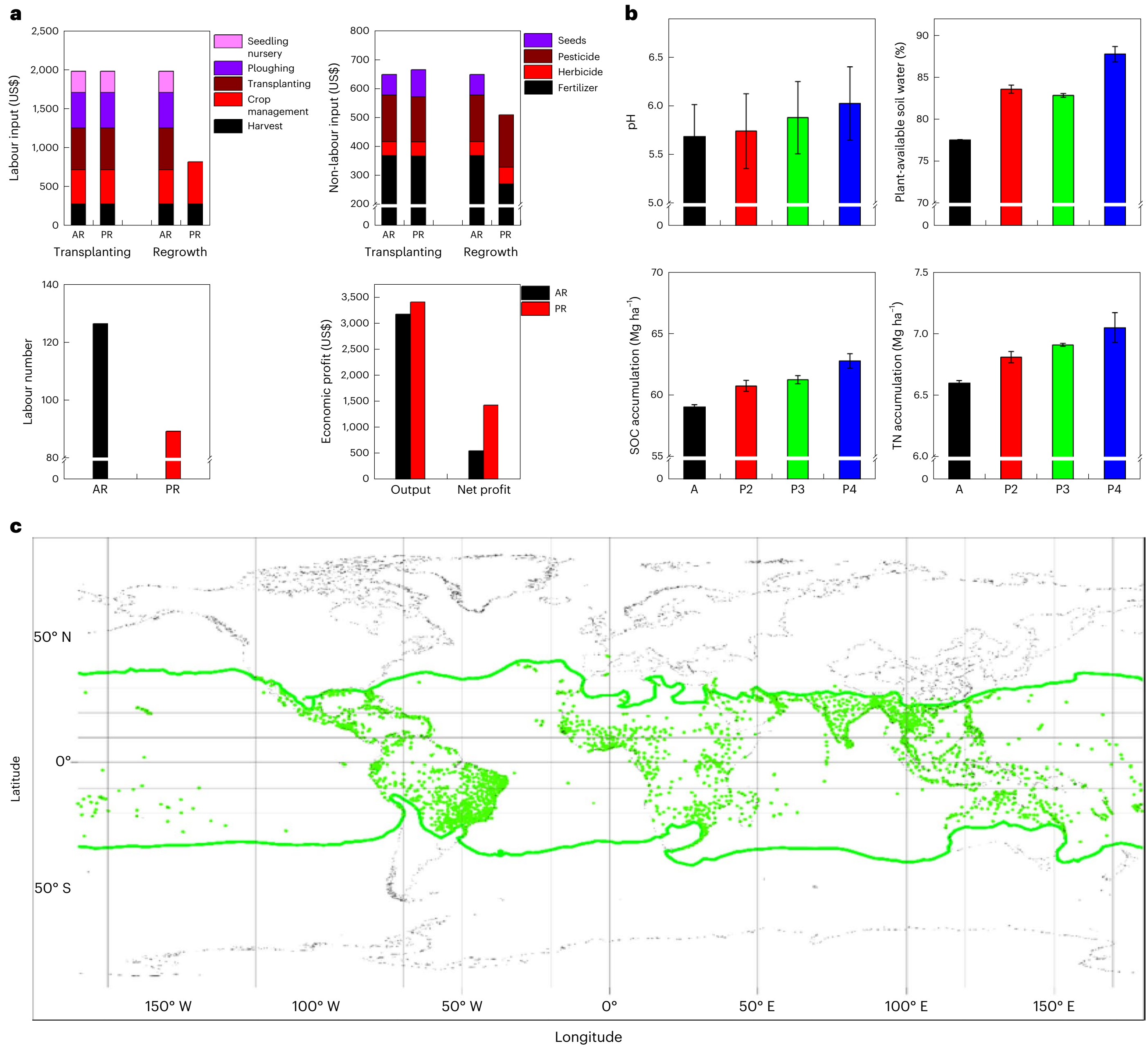

Fig. 3 | Socioeconomic benefits, environmental benefits and potential planting regions of PR. a, Costs in the first and subsequent seasons, labour, outputs (gross income from grain sales) and net profits from AR and PR production. For AR, seed, ploughing, seedling nurseries, transplanting, crop management and harvest are needed in every season. For PR, these are all needed in the first season; however, in the subsequent seasons, tillers of the plant are accomplished by regrowth, and thus seed, seedling nurseries, ploughing and transplanting are not needed, resulting in considerable savings of money and labour. US$1 = CN¥6.4 as of 4 November 2021. The data were derived from Experiment 3, with LSD for labour costs of US$203; non-labour costs, US$203; labour number, 7 days; and economic profit, US$838 ($P < 0.05$) (Supplementary Table 8 and Extended Data Fig. 7). **b**, Soil benefits of perennial rice cropping system. Data are presented for averaged soil pH, total plant-available soil-water capacity (%), soil organic carbon (SOC) accumulation (Mg ha^{-1}) and total nitrogen (TN) (Mg ha^{-1}) accumulation, which have LSDs ($P < 0.05$) of 0.27 units, 1.7%, 1.1 Mg ha^{-1} and 0.2 Mg ha^{-1}, respectively. The error bars represent the standard error of each treatment. The soil properties refer to the 0–40 cm soil layer. PR-2y, PR-3y and PR-4y are perennial rice in years 2, 3 and 4, respectively. Data are from Experiment 3 (Supplementary Table 9 and Extended Data Fig. 8). **c**, Optimal ecological zoning of PR. Data derived from 25,049 meteorology stations, 2015–2020, obtained from the National Centers for Environmental Information (https://ncei.noaa.gov). On the basis of our findings from Experiment 5 (Supplementary Table 10 and 11 and Extended Data Fig. 9), we selected the regions suitable for planting PR, in which the average monthly temperature was higher than 13.5 °C (contours) and in which average daily temperatures lower than 4 °C lasted for fewer than five days (green dots within the contours; 2,695 stations).

reducing drudgery and making the management of the PR production system much easier (Fig. 3a). Equally important is that the reduction in human labour requirements is accomplished without substitution by fossil fuel-based equipment, an important consideration as society aims to reduce greenhouse gas emissions associated with agricultural production. During 2016–2020, the net economic benefits of PR in the regrowth seasons at Mengzhe, Xinping and Menglian averaged US$882, US$109 and US$1,165 ha^{-1} season^{-1}, which were 57.3%, 17.4%

and 161% more than elite AR, respectively (Extended Data Fig. 7i and Supplementary Table 8). Thus, even in the case where yields of PR were significantly lower than AR (for example, Xinping), PR always achieved a greater economic return (Fig. 3a and Extended Data Fig. 7i). This was confirmed by a sensitivity analysis of net economic gain in response to changes in grain yield, labour inputs and cost inputs. For the second crop in the cycle (re-transplanted AR versus the first regrowth cycle of PR), net economic gain was insensitive to changes in labour input or cost input within each system as the major variation in these parameters was between systems. By contrast, net economic gain was highly sensitive to changes in grain yield, with an extra 1 t ha^{-1} transplanted AR generating an extra $436, while an extra 1 t ha^{-1} in each regrowth cycle of PR generated an extra $2,308. Thus, net economic gain was five times as responsive to increase in grain yield in each regrowth cycle of PR than in re-transplanted AR. Adoption of PR 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 AR.

Soil benefits

With soil tillage required for only the initial crop in the cycle, and with less soil disturbance between cycles, PR was expected to provide soil benefits over annual cropping. In the 0–40 cm soil layer, PR cropping over four years resulted in increased soil organic carbon (SOC) and total nitrogen (TN) at rates of 0.95 and 0.11 Mg ha^{-1} yr^{-1}, respectively (Fig. 3b, Extended Data Fig. 8 and Supplementary Table 9). We found that the C/N ratio declined significantly in the topsoil over the years in the perennial cropping system (Extended Data Fig. 8l), which could stimulate microbial decomposition of organic matter and result in net N mineralization in the soil[43]. This predicted enhancement of N cycling due to lower C/N ratios contrasts with apparent net N immobilization of 0.11 Mg ha^{-1} yr^{-1} N, which is a consequence of SOC accumulation following the cessation of tillage[44,45].

The combined effects of no tillage and increases in organic matter under PR appear to have influenced several other key soil properties, including soil pH, plant-available soil-water capacity and capillary and non-capillary porosity (Extended Data Fig. 8b,c). Soil pH increased significantly by 0.3–0.4 units, with all values falling within the optimal range (5.0–6.5) in rice for nutrient uptake (including phosphorus, copper, zinc and boron) and microbial activity (Fig. 3b). This finding supports earlier work[43] that showed SOC stocks of rice paddy soils from 612 sites in 51 countries to be positively correlated with increases in soil pH. Significant increases in plant-available water capacity and porosity have been measured in rice paddy systems with reduced tillage[46], and our measured increases in SOC are also likely to have contributed to greater plant-available soil-water capacity[47] (Extended Data Fig. 8g–i).

In addition, no tillage retains the soil structure, which can enhance the oxidative capacity of soil methane-oxidizing bacteria and thereby reduce methane emissions[40,41], whereas ploughing in annual rice paddies results in an increase of methane emissions by 51.11% (ref. 42). Management of perennial rice with intermittent flooding could further reduce methane emissions by reducing the amount of time soils experience anoxic conditions[48]. However, there may be a trade-off in which intermittent flooding favours substantially greater pulses of nitrous oxide emissions, resulting in higher total global warming potential[48].

Optimal ecological zoning

Low temperature significantly affected the regrowth of PR. In the field experiment, the regrowth rate had a significant quadratic correlation with monthly mean temperature in January 2017 ($y = -2.54x^2 + 86.33x - 633.98$, $R^2 = 0.73^*$, $P < 0.05$) (Supplementary Table 10 and Extended Data Fig. 9a). On the basis of this equation, we used a mean monthly temperature of 13.5 °C in the coldest month as the minimum likely to permit at least 75% regrowth in subsequent PR crops. In the controlled environment experiment, the regrowth percentage of PR decreased from 92.2% to 55.4% when temperatures of 4 °C lasted for seven days, while regrowth decreased to 82.8% after five days and 22.4% after seven days at 0 °C ($P < 0.05$) (Supplementary Table 11 and Extended Data Fig. 9b). From these results, we determined that periods with an average daily temperature lower than 4 °C must last for fewer than five days for PR regrowth to be likely to remain above 75%.

On the basis of these findings for low-temperature effects on regrowth, we assessed which of 25,049 meteorological stations from the National Centres for Environmental Information (https://ncei.noaa.gov) met the criteria. The climates in 2,659 stations were considered potentially suitable for PR cultivation on the basis of cardinal temperatures for regrowth. This suggests that PR has a broad range of potential planting regions, generally within the latitudes of 40° N and 40° S (Fig. 3c).

We recognize that high temperature affecting spikelet fertility around flowering would also impose limits on zones for PR cultivation. Jagadish et al.[49] reported that spikelets in rice became sterile when exposed to 33.7 °C around anthesis, although reductions commenced from 29 °C. From meiosis to anthesis to early grain expansion, Nguyen et al.[50] reported spikelet sterility commenced as spikelets were exposed to 31 °C from 12 days before anthesis to 12 days after anthesis. Consequently, we conclude that exposure to temperatures of about 31 °C during the month around flowering would be detrimental to spikelet fertility in rice, and the zoning analysis should be extended for these high-temperature limitations. Nevertheless, the estimated ranges of PR and AR are likely to be similar based on temperature alone as cardinal temperatures are considered to be species characteristics[51]. When other factors (precipitation, evapotranspiration, landscape) are included, however, the range of AR will decline as PR will better cope with abiotic stress (due to extensive root systems and greater assimilate reserves) and in more marginal landscapes (due to lack of soil disturbance, continued soil cover, reduced leaching and nutrient loss, and reduced run-off and soil loss, with run-off and soil loss being of major concern in the sloping rainfed uplands).

Prospects and potential

After more than 20 years of effort, the cultivation of PR has become a reality. This represents a cropping system that simultaneously achieves grain production, labour reduction and ecological security, especially for terraced and fragile farmland. PR has demonstrated good yield potential, and agronomic traits for four years and eight cropping seasons from a single planting can enhance soil fertility and reduce requirements for inputs through ecological intensification. The simplified management, reduced labour requirements and improved livelihood made possible by PR are attractive, so this technology is becoming accepted by increasingly more farmers. This is particularly important because in most countries, rural labour forces have declined due to migration of people to cities, and the application of PR will undoubtedly relieve the work burden of rural farmers, especially women and children, who often provide the unskilled labour[52].

Given the recent development of PR, numerous important research questions are just beginning to receive attention. For example, we found more herbicide applications were required in regrowth cycles than in transplanted AR, suggesting the need for improved weed-management agronomy. And while not encountered here, pests adapted to high N applications could pose threats in irrigated systems, especially if pustule loads in stubble were large or insect-transmitted viruses became established in regenerating plant crowns (Performance and adoption and Methods). Finally, understanding management practices that influence the total emissions and relative balance of methane and nitrous oxide trace gasses is critical for understanding total global warming potential of this crop.

Our PR has received certification for commercialization due to the multifaceted benefits it brings, providing a promising solution that reconciles food production with environmental security and the needs of farmers. Recent advances in plant breeding, such as low-cost DNA sequencing, molecular marker-assisted selection, genomic selection and gene editing, can be expected to further accelerate the development of PR in the future, as well as facilitate the perennialization of other crops. Having succeeded in developing a PR adapted for irrigated and favourable lowland conditions, we have now begun breeding PR cultivars suitable for rainfed lowland and importantly for rainfed upland cultivation. PR has great potential for curbing serious erosion and other forms of soil degradation that are common in such marginal lands, especially in upland regions of Southeast Asia[53].

Methods

Rice ecosystems and cultural practices

Characteristics of rice ecosystems and their cultural practices have recently been reviewed by Fukai and Wade[29]. Briefly, rice ecosystems are commonly classified by water availability. The most common is irrigated lowland, in which the paddy field is shallow-flooded after the crop is established until just before harvest. Another major ecosystem is rainfed lowland, in which fields are bunded like in irrigated to maintain ponded water, but with no or limited irrigation, conditions can vary depending on rainfall. Soils may be saturated and anaerobic during the growing season, but in periods of low rainfall, ponded water vanishes, the soil becomes aerobic, and plants quickly encounter water deficit. In flood-prone ecosystem, rice may be submerged, and deep-water or floating rices may be grown. Conversely in upland ecosystem, ponded water is absent, and rice is grown in aerobic soil sometimes on sloping land.

Irrigated rice has traditionally been transplanted into puddled soil, which is cultivated wet to reduce drainage and enhance ponding of water. Transplants have a competitive advantage over newly-emerging weeds, which generally die from anaerobiosis. In addition, soil nutrient availability is improved by puddling, and the paddy favours development of complex food webs for IPM. The disadvantages include labour-intensive cultivation and transplanting, high water use and greenhouse gas emissions and difficulty in establishing post-rice crops into previously puddled soils. Direct seeding into non-puddled soil, and flush irrigation, with ponded water restricted to critical growth phases, have been employed to reduce these problems, although early nutrient availability and weed problems have increased as a consequence. Double cropping of AR is common where temperatures are favourable, and rainfall or irrigation is sufficient. Where cooler conditions are encountered at higher altitude or latitude, however, only one rice crop per year may be harvested from the first season (dry season, December to May in our locations). Conversely, where hotter and drier conditions are encountered, only one rice crop per year may be harvested from the second season (wet season, June to November). PR offers the potential to produce several crop cycles from a single planting, with performance in regrowth cycles dependent on successful survival, regrowth, spikelet fertility and grain yield in the conditions encountered[29].

Experimental approach

We conducted five experiments to explore the potential and benefits of PR across field locations in China (Supplementary Table 12). In Experiments 1 and 2, we studied genotype-by-environment interactions from multi-environment trials to examine the effects of selection during breeding, enabling us to estimate variance components and heritability to elucidate patterns of PR adaptation. In Experiment 3, large-plot trials were used to study the performance, long-term productivity and livelihood benefits of PR23, the first PR cultivar released. Trials of PR25 and PR107, subsequent PR releases, were conducted to quantify performance over years and locations (Experiment 4). Finally, PR23 was used to evaluate conditional cold tolerance of PR (Experiment 5). Experimental designs, treatments, cultural practices, data collection and analysis, mean yield and sources of further information are summarized for Experiments 1–4 in Supplementary Table 6, with the main attributes explained briefly for each experiment in the following. Soil constraints, pests, diseases and weeds may pose threats to successful perennial rice cropping, so the following section considers the risks they pose and the mitigation strategies available. Finally, we provide details for socioeconomic and soil measurements and details of the statistical analysis.

Experiment 1

Field trials were conducted in 12 location–season–year (environment) combinations at Jinghong, Menglian and Simao in Yunnan Province of China and at Na Pok in Vientiane Province of Laos in 2012 and 2013. At each location, a randomized complete blocks design was used, comprising 22 genotypes with 2–3 replicates. The 22 genotypes comprised PR derivatives obtained from the cross between *O. sativa* cultivar RD23 and the wild species *O. longistaminata*. Specific details about the development of these breeding lines were reported by Zhang et al.[54]. There were two crops per year at Jinghong and Menglian, but only one crop per year at Simao (first season) and Na Pok (second season). Cultural, measurement and analysis details are summarized in Supplementary Table 6. Briefly, after each harvest, stubble was cut to 10 cm so that consistent stubble for uniform regrowth was available. Mean timings of transplanting and maturation and successive cycles of stubble cut-off and maturation were recorded to define growth duration in each cycle. Regrowth percentage, plant height, grain yield and yield components were recorded from each plot, from 0.9 m^2 samples[31].

Experiment 2

The trials were conducted in 19 environment combinations at Jinghong, Puer (Simao), Hongta, Wenshan, Yuanyang, Lancang and Dehong in Yunnan Province of China in 2014–2016. The trials at Jinghong (double crop) and Puer (first season) were continued for three years while the others (first season) continued for two years only. At each location, the trial was a randomized complete blocks design comprising nine genotypes with three replications. Five PR genotypes thought to differ in adaptation[31], obtained from the cross between *O. sativa* cultivar RD23 and the wild species *O. longistaminata*, were included, along with three annual *O. sativa* cultivar controls[32]. Cultural, measurement and analysis details were similar to Experiment 1, except a split dressing of 72 kg ha^{-1} N was applied at boot stage (Supplementary Table 6)[32].

Experiment 3

In this field experiment, larger plots of PR23 of 1–13 ha were grown to examine performance, socioeconomics and impact of PR versus AR lines for validation and official release purposes, at Mengzhe, Menglian and Xinping in southern Yunnan province of China, with data collected from 2016 to 2020. Double cropping is the dominant rice cropping system at all three locations, which have a subtropical monsoon climate with mean annual temperature of 18–19.6 °C. The annual rainfall is 869–1,341 mm, which falls mainly in the second season from May to October. The PR PR23 was compared with locally elite AR cultivars selected specifically for each location, which, for Mengzhe, Xinping and Menglian, were Diantun502, Yunhui290 and Wenfu6, respectively (Supplementary Table 6).

Both PR23 and AR were established in the seedling nursery and transplanted to the field. After the first harvest, the straw of PR was cut back to 10 cm above the ground to maintain the uniformity of new tillers arising from rhizomes and to depress tillers from developing from above-ground nodes in each season, with no till being conducted across the successive regrowth cycles. By contrast, for AR, the rice stubble was ploughed after each harvest and the rice was seeded and transplanted as it was in the first season, which is a typical commercial practice in the region. At each location, PR and AR were planted in adjacent plots within the same ecological area. The rice fields were managed by the local farmers under our guidance. During the growth

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season of PR and AR, the labour and non-labour costs were recorded. At each harvest, yield-related traits (grain yield, duration, regrowth rate, panicle number m^{-2}, spikelet number $panicle^{-1}$, grain weight and seed-setting rate) were measured.

Experiment 4

Field trials were conducted in Yunnan Province, China, at seven locations: Mengzhe, Menglian, Jinghong, Xinping, Lancang, Wenshan and Yiliang. Measurements at these locations took place over the course of three years, from 2018 to 2020. The management of PR was the same as in Experiment 3. PR25 and PR107 were selected as experiment material, and PR23 as selected as control. At each harvest, yield-related traits (grain yield, duration, plant height, regrowth rate, panicle number m^{-2}, spikelet number $panicle^{-1}$, grain weight and seed-setting rate) were recorded (Supplementary Table 6).

Experiment 5

Two sub-experiments were conducted to assess the regrowth potential of PR in response to low temperature, with an initial field experiment followed by a controlled-temperature chamber experiment. The first experiment was conducted at 16 field locations in 2016 and 2017 (Supplementary Table 10). At each location, a ratoon crop was exposed to low temperatures in the field in January during early regrowth, and mean monthly temperature and regrowth percentage were recorded. A quadratic equation was fitted to the relationship between temperature and regrowth percentage, and LSD for regrowth percentage ($P < 0.05$) was obtained.

The second experiment was conducted in a low-temperature plant incubator (model FH-1300, Taiwan Hipoint Co. Ltd) at Yunnan University. Individual plants in 1 cm pots with three replicates were exposed to temperatures of 0 °C or 4 °C for three, five or seven days from the three-leaf stage. Regrowth percentage was recorded for each plant, and means and LSD ($P < 0.05$) were obtained.

Critical temperatures identified from the two sub-experiments on low-temperature effects on regrowth were then used to assess potential ecological zones for PR. Data from 25,049 meteorological stations worldwide (National Centres for Environmental Information, https://ncei.noaa.gov) were assessed using these criteria, and stations that met the criteria were mapped using GIS to identify potential ecological zones for PR worldwide.

Risks and mitigation

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 Data Fig. 4), suggesting PR would need to be resown after about four years. We observed that although the regrowth rate showed a decreasing trend over ten seasons, the panicle number m^{-2} and other grain yield traits were maintained. This indicates an ability of PR to regrow and tiller, which can compensate for the minor decrease in plant stand that may occur in earlier regrowth cycles. In the fifth year (the ninth and tenth seasons), however, grain yield decreased significantly due to a significant decrease in regrowth rate (below 75%), panicle number and spikelet number per panicle (Extended Data Fig. 4). Present cultivars of PR would need to be resown in year 5, preferably by direct seeding into minimum or zero tillage, with stubble cut to a height of 10 cm and excess straw removed if necessary for passage of machinery. Alternatively, PR could be rotated with a legume pasture or a pulse or brassica crop to provide a break from pests, diseases and weeds and to support other farm enterprises such as livestock.

While low temperatures in winter[31] or high temperatures and drought in summer[55] may reduce regrowth or kill the plant, perennial stubble may also need to be killed under favourable conditions to establish a new crop. Short rhizomes were selected intentionally in PR so as not to provide significant weed potential but to permit improved chances of survival when harsher conditions are encountered. Under irrigation, therefore, tillage may be required to expose the crowns of PR to soil drying, perhaps with follow-up glyphosate spraying of young regrowth if needed before re-sowing. In addition, post-rice crops on puddled soil may encounter difficulties from poor soil structure[29], but this problem may be reduced after several ratoon cycles as soil structure parameters generally improved here (Supplementary Table 9). This problem would be minimized by establishing PR by direct seeding without soil puddling, which is becoming more common in rice, especially under conditions of labour scarcity[56].

Pests and diseases of rice have been extensively studied. Under irrigated conditions, breakouts of brown plant hopper, green leaf hopper and leaf folder are associated with high N application but can be managed through integrated pest management with split applications of N more closely matching crop demand[57]. Rust, blast and other leaf and panicle diseases can be severe, but resistance is available in many rice cultivars, and crossing with *O. longistaminata* may provide additional resistance. These strategies should also be effective for PR. Under rainfed cultivation, pests and diseases are usually less severe although gall midge can be important if ponded water is absent during tiller elongation, and thrips can be damaging locally[58]. Perhaps of greater concern are insect-transmitted viruses that would remain viable in crowns and diseases with a high pustule load able to re-infect from previous stubble. Viruses of concern may include tungro[59] and rice yellow mottle virus in Africa, although PR107 is resistant to the latter from its *O. longistaminata* parent and has been released in Uganda. Nevertheless, an additional one to two sprays were needed for weed control in regrowth cycles of PR in our experiments, relative to re-transplanted AR (Supplementary Table 6).

In perennial cropping systems, weeds are often observed to build up over cycles, but this may be of less concern in irrigated rice systems, in which timely soil flooding suppresses or kills most weeds early in each crop cycle. Some weeds adapted to anaerobic conditions may survive[60], but grazing by ducklings when seedlings are small[56] or after harvest by livestock can suppress weeds, together with spot spraying of remaining problems with glyphosate if needed.

Livelihood benefits

In Experiment 3, cooperating farmers were surveyed to establish the timing and details of cultural practices, labour requirements and labour and non-labour costs, which were recorded for both PR and AR systems. The total labour number (persons ha^{-1}) was confirmed by dividing total labour cost (US$ ha^{-1}) by labour price (US$15.63 $person^{-1}$ on 4 November 2021). Total output was calculated as the product of grain yield and market price (AR, US$0.55 kg^{-1}; PR, US$0.48 kg^{-1} on 4 November 2021). Net economic gain was obtained by difference, from output minus input.

Soil benefits

Soil samples were collected with three replications after rice harvest in December each year. Core samples for soil nutrients and soil physical properties were obtained over four soil depth increments (0–10, 10–20, 20–30, 30–40 cm) under the PR and AR systems. Soil bulk density was measured from undisturbed cores of known volume, at saturation (upper limit (UL)) and at wilting point (lower limit (LL)) of rice. Undisturbed cores were weighed, dried in a convection oven at 105 °C for 24 hours and weighed again to determine volumetric soil water contents at UL and LL and plant-available water capacity (UL − LL) for each depth increment. From these data, bulk density and soil porosity were also calculated.

Soil nutrients

For soil chemical analysis, core samples were sieved through a 0.25 mm screen. SOC was extracted using the K_2CrO_7–H_2SO_4 heat treatment, and residue was determined using the $FeSO_4$ titration of potassium dichromate method[61]. Soil TN was determined using the Kjeldahl method[62].

The total accumulations of SOC and soil nitrogen were calculated as the product of SOC × bulk density and TN × bulk density over depth increments, respectively.

Statistical analysis

Genotype-by-environment interactions were examined by joint application of cluster and ordination analysis using CropStat 7.2 (IRRI, http://bbi.irri.org), with further details of those analyses provided elsewhere for Experiment 1[31] and Experiment 2[32]. Variance components and heritability were also obtained for all parameters from both experiments. For the crop yield data and soil properties, the mean values were calculated for each measurement, and analysis of variance was used to compare the effects of different treatments on the measured variables, with comparisons performed using the LSD test ($P \leq 0.05$). LSD is the product of $t_{0.05}$ and the square root of $2s^2/r$, where $t_{0.05}$ is the tabular value of Student's t for error degrees of freedom at a probability of 0.05, s^2 is the pooled error variance, and r is the number of observations per mean. All LSD tests were two tailed, and no adjustments were made for multiple comparisons. Experimental data were analysed with the IBM SPSS statistical package v.20.0 (SPSS, Inc.), and the figures were generated using Origin 2015 (Sys Software, Inc.).

Reporting summary

Further information on research design is available in the Nature Research Reporting Summary linked to this article.

Data availability

The data supporting the findings of this study are available within this paper and the Supplementary Information. Source data are provided with this paper.

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Author contributions

F.H. and L.J.W. designed the research. S.Z., G.H. and Y.Z. were key players for the field trials. X.L., K.W., J.L., Y.F., J.D., S.W., L.Z. and X.Y. helped organize the field trials in Yunnan Province. S.Z., G.H., Y.Z., X.L., L.H., L.S., J.Z., S.Q., D.T. and L.J.W. collected and analysed the data. S.Z., G.H., Y.Z., E.J.S., T.E.C., J.L., L.J.W. and F.H. interpreted the data and wrote the manuscript.

Competing interests

The authors declare no competing interests.

Additional information

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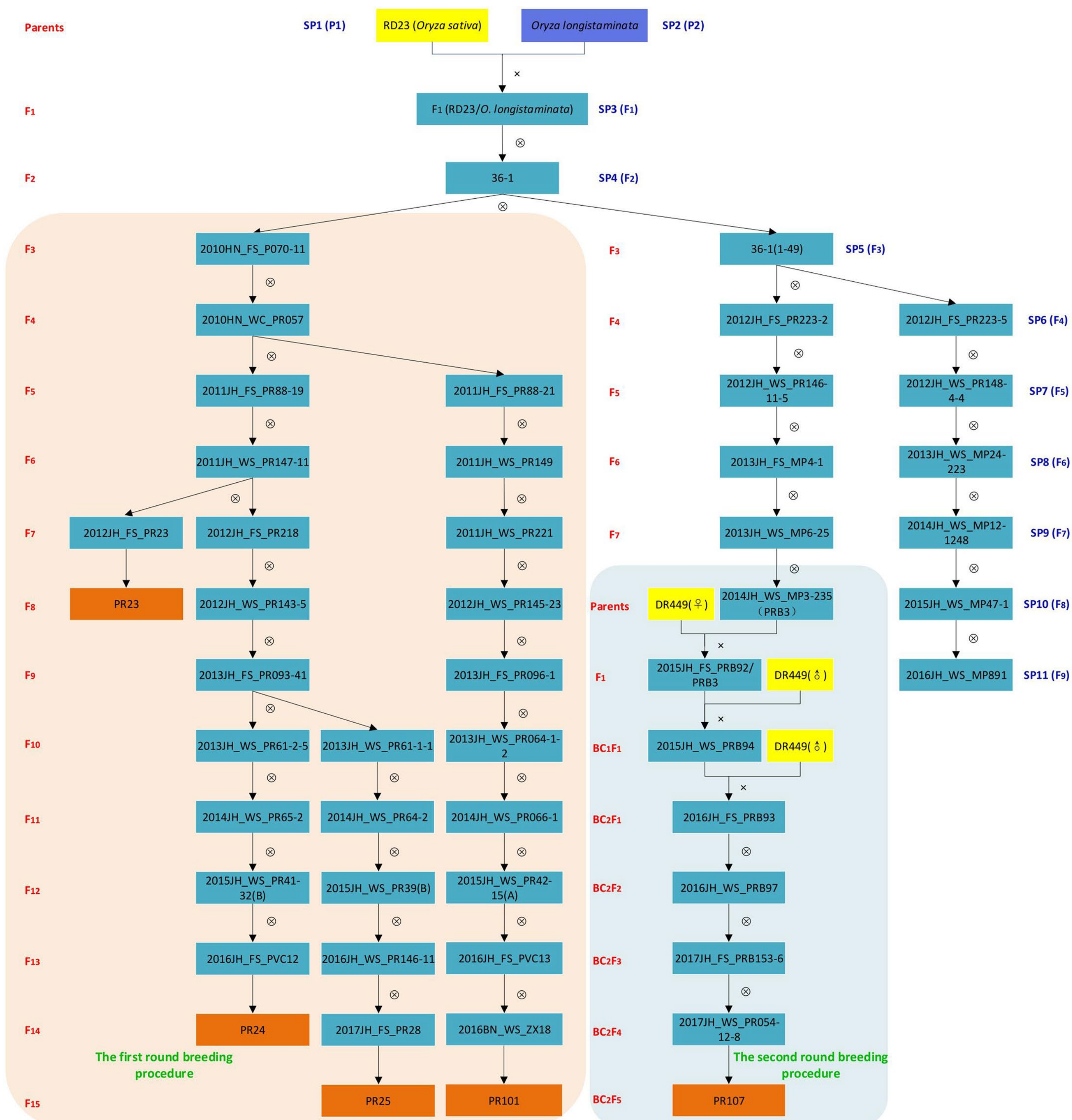

Extended Data Fig. 1 | Breeding of perennial rice. JH and HN refer to Jinghong Station in Yunnan and Hainan Station in Sanya, Hainan, China. FS, first (that is, hot and dry) season; WC or WS, second (that is cool and wet) season in double-crop regions. Red font indicates the different generations. SP1 is *Oryza sativa* spp. *indica* RD23 (P1), SP2 is *O. longistaminata* (P2), and SP3 is RD23 / *O. longistaminata* (F_1). SP4 to SP11 are single individuals selected from the previous generation, with both good fertility and good rhizome characteristics. Yellow boxes indicate *O. sativa*, purple box indicates *O. longistaminata*, blue boxes indicate interspecific breeding lines, and orange boxes indicate interspecific cultivars. The numbers of plants evaluated in each generation from F_1 to F_{15} were 1, 1, 1, 7,200, 1,250, 57, 78, 104, 384, 864, 100, 1,078, 1,294, 1,572, 1,403, 1,520 and 1,105, respectively.

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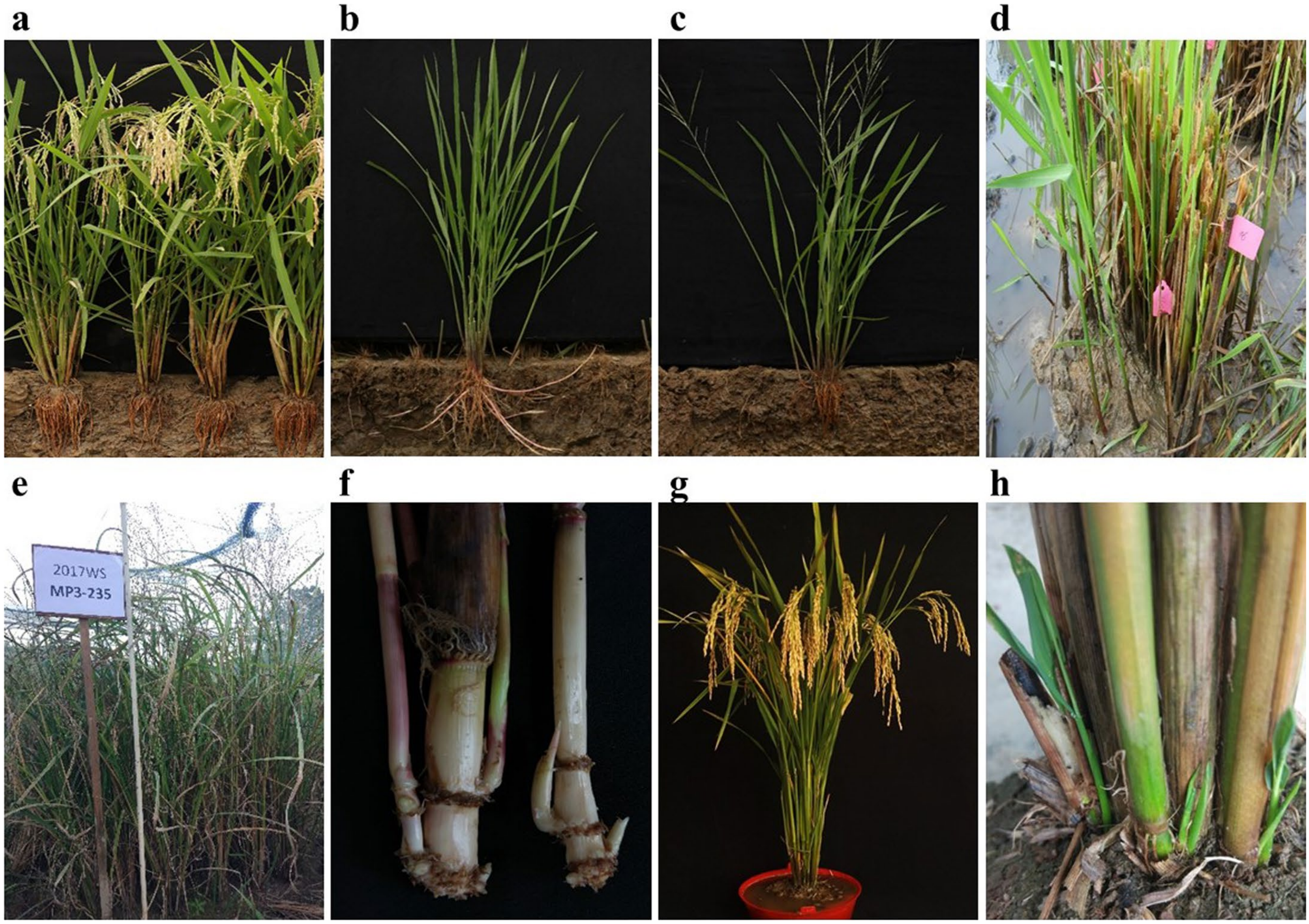
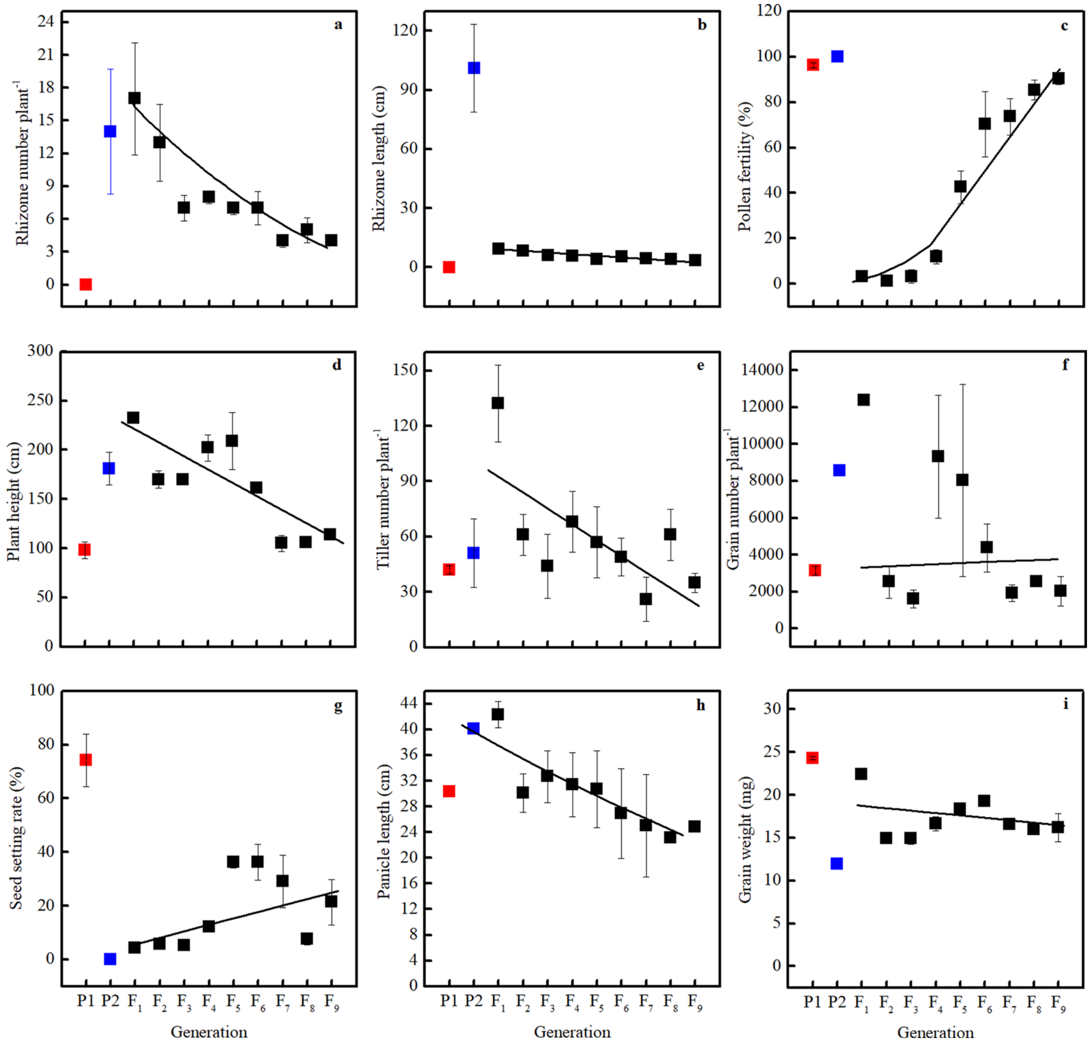
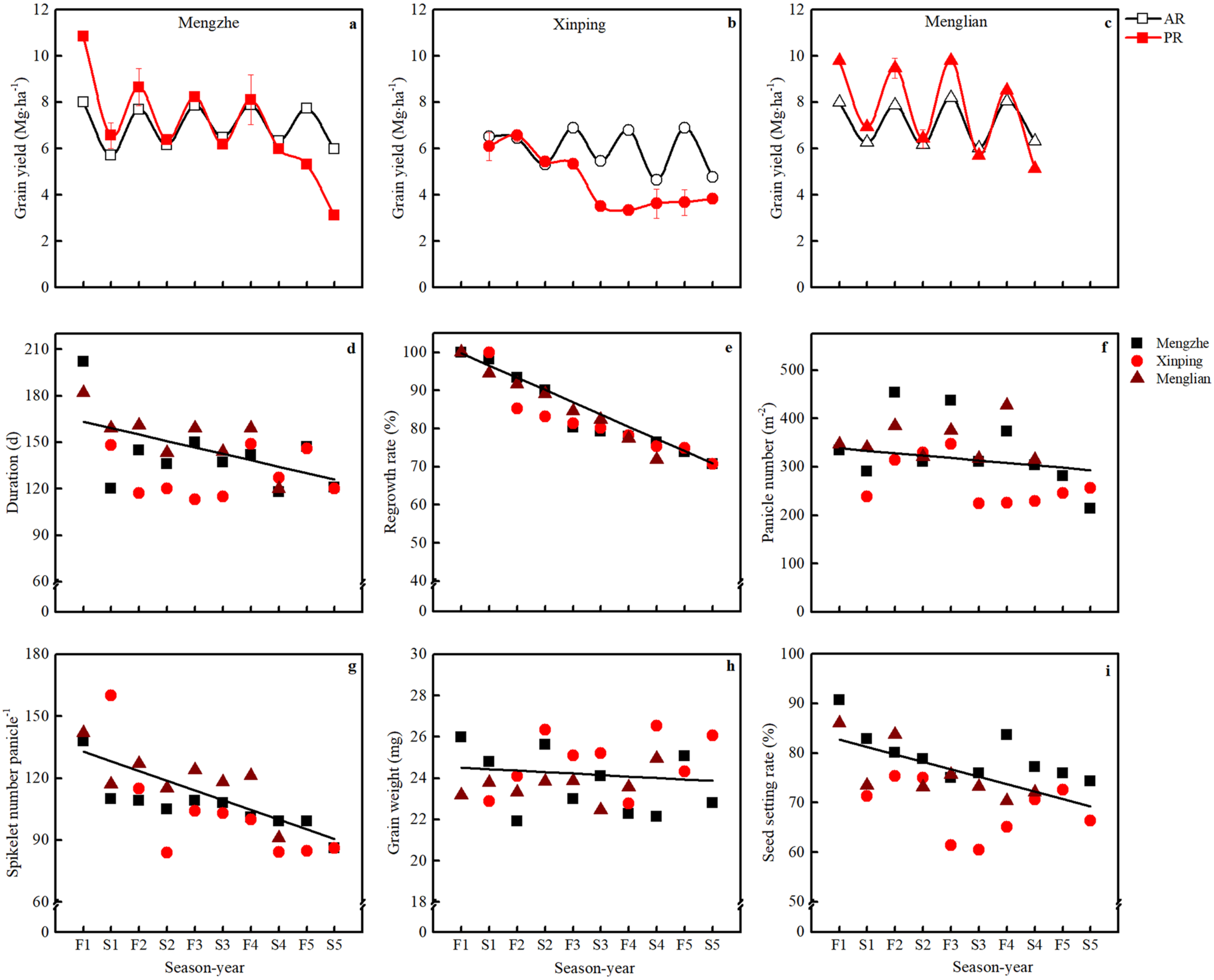


Extended Data Fig. 2 | Selecting elite breeding lines of perennial rice with strong perenniality. a, *O. sativa* RD23 as female parent. **b**, *O. longistaminata* as male parent. **c**, F_1 (interspecific hybrid between RD23 and *O. longistaminata*). **d**, 36–1 (F_2 individual derived from F_1). **e-f**, MP3–235 (F_9 individual chosen as a breeding line donor of perenniality for breeding), with desirable short rhizomes, but showing other undesirable agronomic traits, including plant height over 2 m and strong seed shattering. **g**, Perennial rice cultivar PR107 at maturity. **h**, PR107 regrowth 3 days after harvest.



Extended Data Fig. 3 | Changes in agronomic traits over generations of breeding perennial rice. a, Rhizome number (plant^{-1}). **b**, Rhizome length (cm). **c**, Pollen fertility (%). **d**, Plant height (cm). **e**, Tiller number (plant^{-1}). **f**, Grain number (plant^{-1}). **g**, seed setting rate (%). **h**, Panicle length (cm). **i**, Grain weight (mg). P1, *O. sativa* RD23 as female parent (red). P2, *O. longistaminata* as male parent (blue). F_1–F_9 (black). The error bar represents the standard error of each treatment. Data are presented as means, and l.s.d. for the traits are: a) 4; b) 9.6; c) 2.4; d) 2; e) 20; f) 2,753; g) 7.6; h) 3.0; and i) 1.0 (N = 33; $P < 0.05$) (see Supplementary Table 1).



Extended Data Fig. 4 | Comparison of grain yield and agronomic traits of perennial rice cultivar PR23 from a single planting and replanted annual rice seasonally over five years with 10 seasons during 2016–2020. The experiment was conducted at three field trial locations in Yunnan, China: Mengzhe (21°57′ N, 100°14′ E, 1,255 m), Xinping (24°02′ N, 101°34′ E, 760 m) and Menglian (22°33′ N, 99°59′ E, 980 m). **a-c**, Grain yield of annual rice replanted from seed each season and perennial rice planted once in 2016 at three field trial locations (Mg ha^{-1}). The error bar represents the standard error of each treatment. **d**, Duration of perennial rice (d). **e**, Regrowth rate of perennial rice (%). **f**, Panicle number m^{-2} of perennial rice. **g**, Spikelet number $panicle^{-1}$ of perennial rice. **h**, Grain weight of perennial rice (mg). **i**, Seed setting rate of perennial rice (%). F1–F5 represent the first seasons of years 1–5. S1–S5 represent the second seasons of years 1–5. The elite annual rice cultivars for Mengzhe, Xinping and Menglian were Diantun502, Wenfu6 and Yunhui290, respectively, and all three locations are double cropping paddy areas. The data are means from Experiment 3, with l.s.d. for these traits being: a-c) 1.7; d) 22; e) 4; f) 96; g) 18; h) 2; and i) 9 (N = 81; $P < 0.05$) (see Supplementary Table 4).

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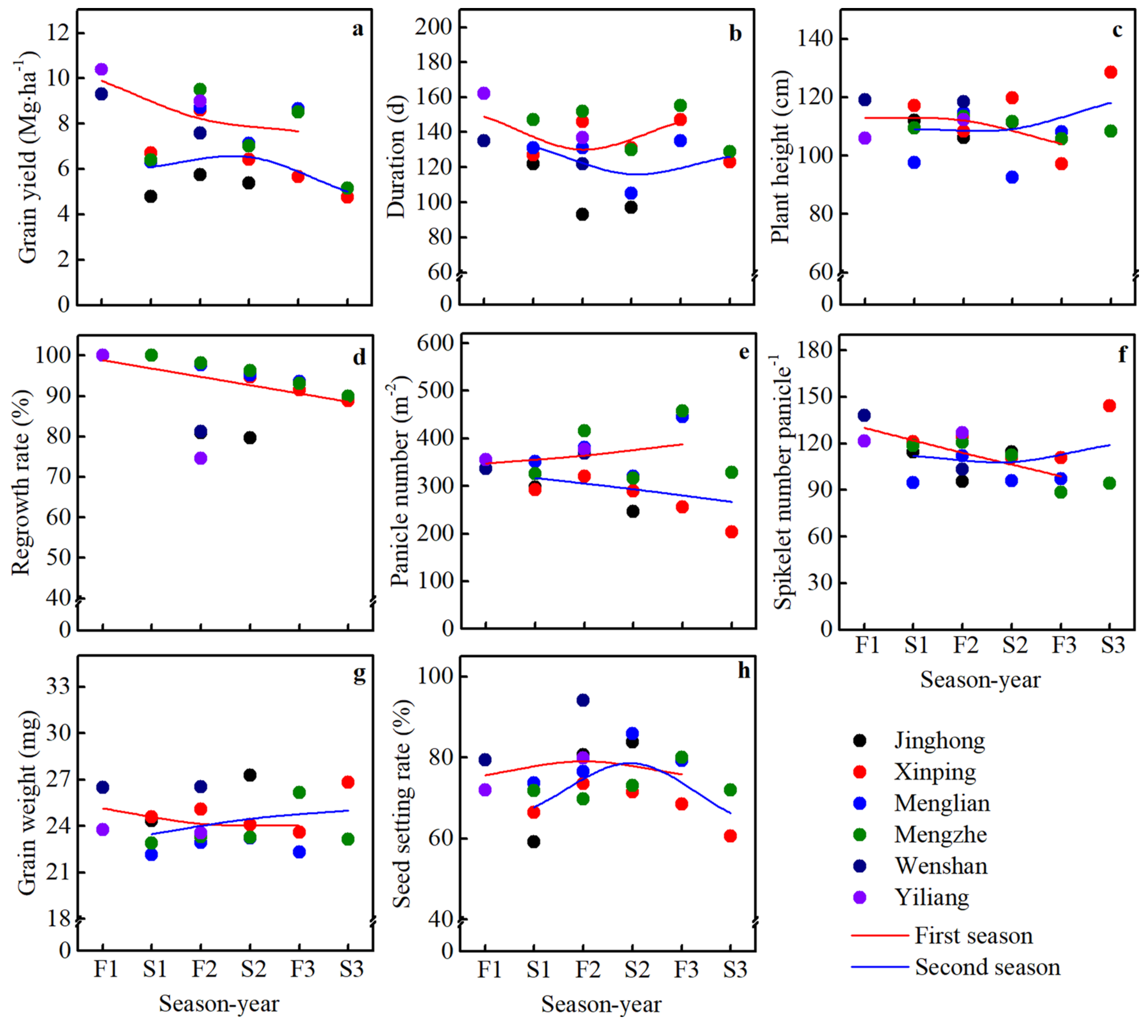

Extended Data Fig. 5 | Grain yield and agronomic traits of perennial rice cultivar PR25 over three years at six locations. **a**, Grain yield (Mg ha^{-1}). **b**, Duration (d). **c**, Plant height (cm). **d**, Regrowth rate (%). **e**, Panicle number m^{-2}. **f**, Spikelet number panicle^{-1}. **g**, Grain weight (mg). **h**, Seed setting rate (%). Field trial locations were double cropping paddy areas in Jinghong (21°59′ N, 100°44′ E, 550 m), Menglian (22°33′ N, 99°59′ E, 960 m), Mengzhe (21°57′ N, 100°14′ E, 1,255 m) and Xinping (24°02′ N, 101°34′ E, 600 m) and single cropping paddy areas in Wenshan (23°23′ N, 104°13′ E, 1,260 m) and Yiliang (24°54′ N, 103°09′ E, 1,600 m). F1–F3 represent the first seasons of years 1–3. S1–S3 represent the second seasons of years 1–3. The data are means from Experiment 4, with l.s.d. for these traits being: a) 1.2; b) 17; c) 8; d) 7; e) 56; f) 14; g) 2; and h) 7 (N = 63; $P < 0.05$) (see Supplementary Table 5).

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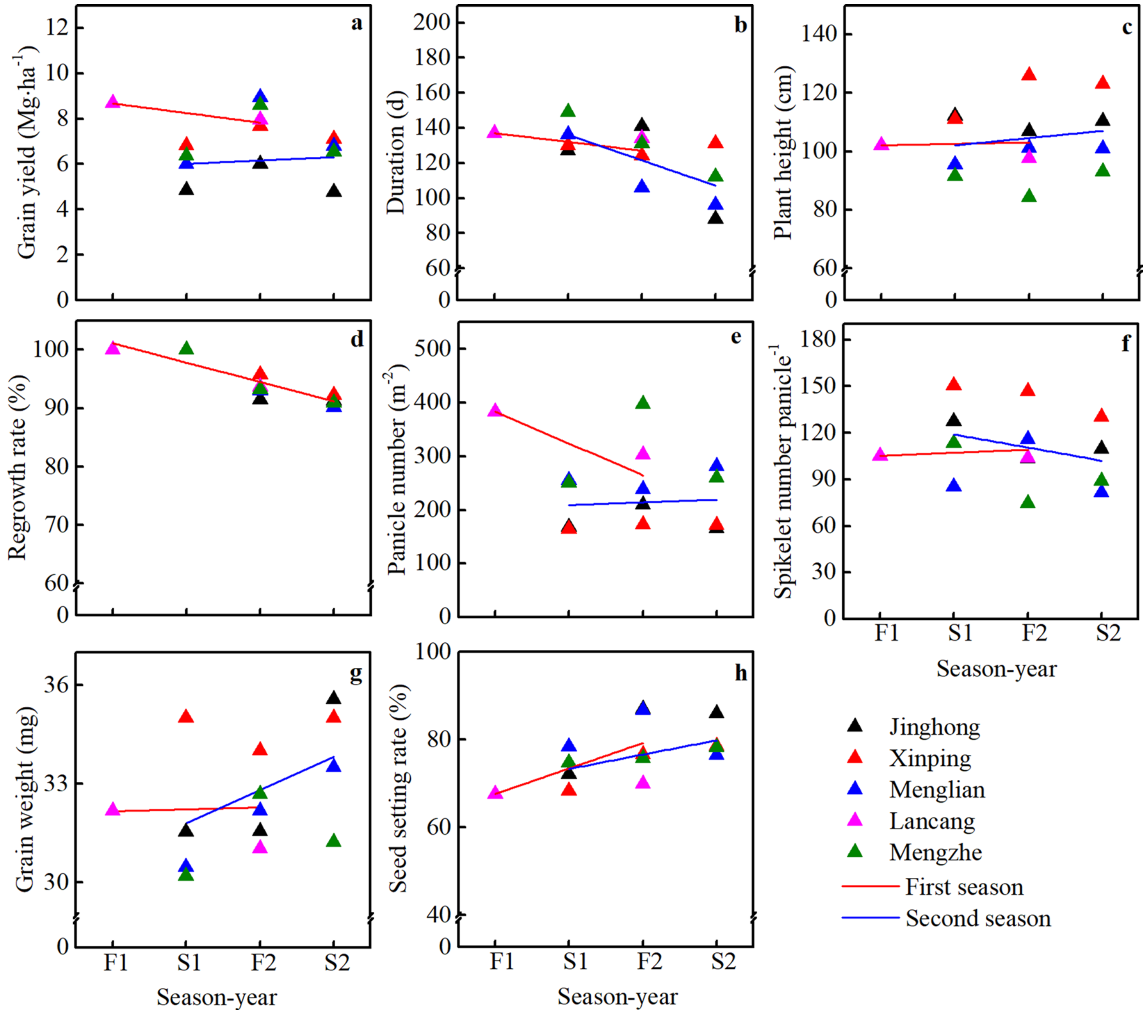

Extended Data Fig. 6 | Grain yield and agronomic traits of perennial rice cultivar PR107 over two years at five locations. a, Grain yield (Mg ha^{-1}). **b**, Duration (d). **c**, Plant height (cm). **d**, Regrowth rate (%). **e**, Panicle number m^{-2}. **f**, Spikelet number panicle^{-1}. **g**, Grain weight (mg). **h**, Seed setting rate (%). Field trial locations were double cropping paddy areas in Jinghong (21°59′ N, 100°44′ E, 550 m), Menglian (22°33′ N, 99°59′ E, 960 m), Mengzhe (21°57′ N, 100°14′ E, 1,255 m) and Xinping (24°02′ N, 101°34′ E, 600 m) and a single cropping paddy area in Lancang (22°26′ N, 99°58′ E, 1,020 m). F1–F2 represent the first seasons of years 1–2. S1–S2 represent the second seasons of years 1–2. The data are means from Experiment 4, with l.s.d. for the traits being: a) 1.2; b) 17; c) 15; d) 1; e) 81; f) 29; g) 2; and h) 7 (N = 42; $P < 0.05$) (see Supplementary Table 5).

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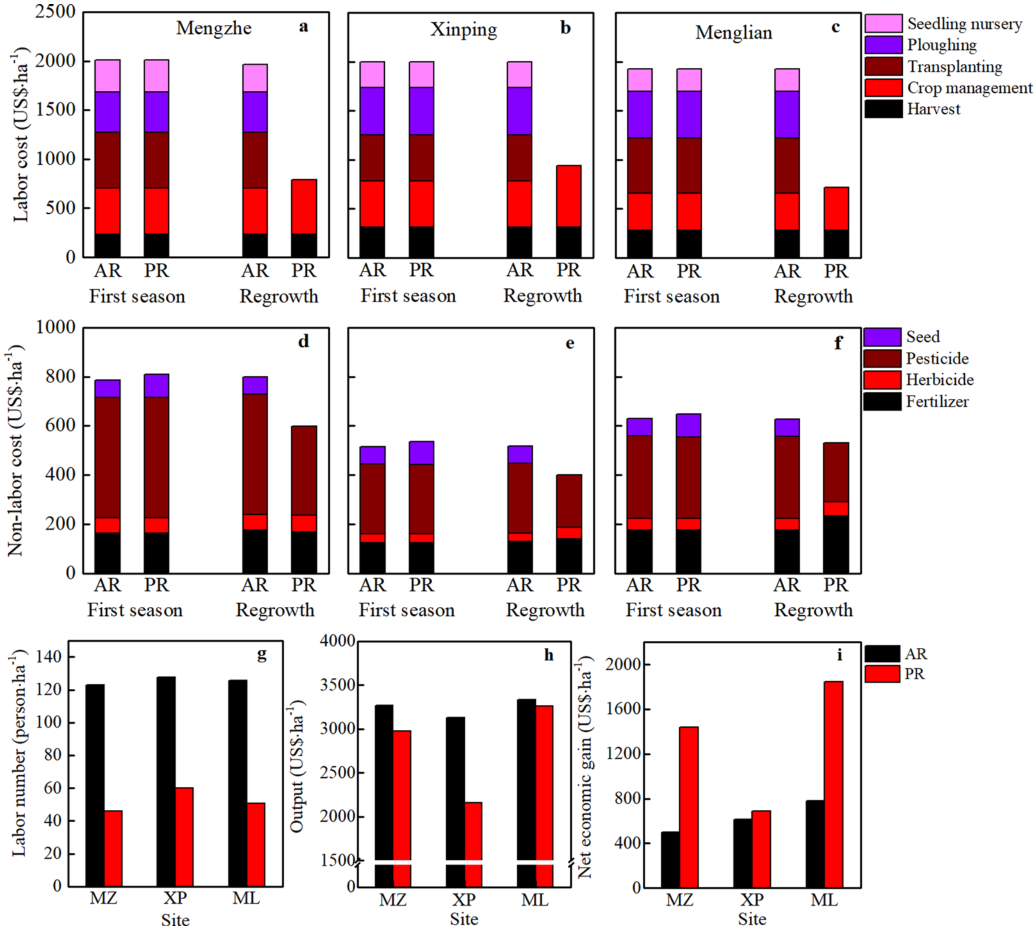

Extended Data Fig. 7 | Comparisons of livelihood benefits between perennial rice (PR) and annual rice (AR) cropping systems over five years with ten seasons. The experiment was conducted at three field trial locations in Yunnan, China: Mengzhe (MZ; 21°57′ N, 100°14′ E, 1,255 m), Xinping (XP; 24°02′ N, 101°34′ E, 760 m) and Menglian (ML; 22°33′ N, 99°59′ E, 980 m). **a-c**, Labour cost ($). **d-f**, Non-labour cost ($). **g**, Labour number input (d). **h**, Output (gross income $). **i**, Net economic gain ($). For annual rice, seed, ploughing, seedling nurseries, transplanting, crop management and harvest are needed in every season. For perennial rice, these are all needed in the first season; however, in the subsequent seasons tillers of the plant are accomplished by regrowth, and thus seed, seedling nurseries, ploughing and transplanting are not needed, resulting in considerable savings of money and labour. 1 US$ = 6.4 Chinese Yuan, as of 4 November 2021. The data are means from Experiment 3, with the l.s.d. for labour cost being 101; non-labour cost, 102; labour number, 7; output, 886; and net economic gain, 838 (N = 54; $P < 0.05$) (see Supplementary Table 8).

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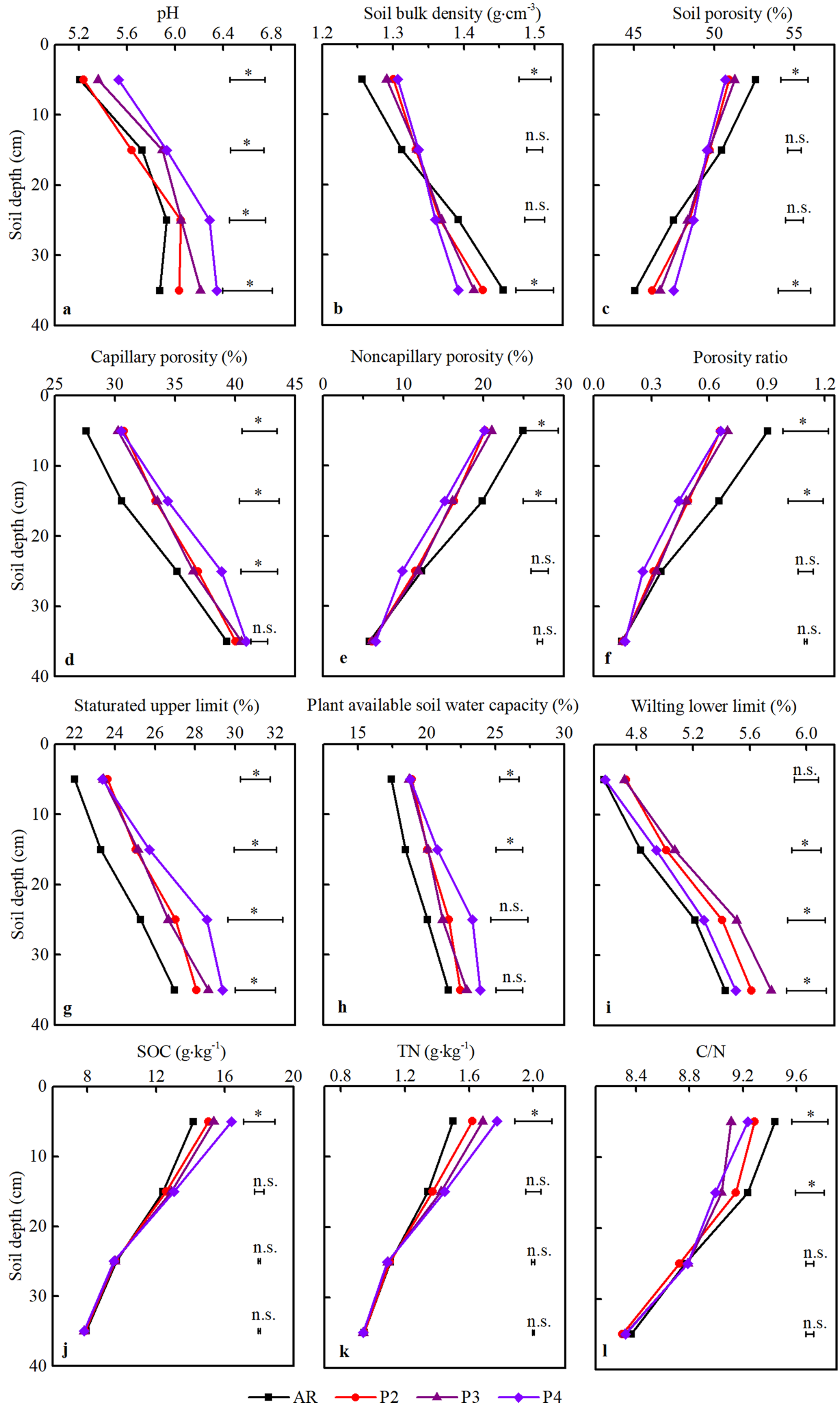

Extended Data Fig. 8 | See next page for caption.

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Extended Data Fig. 8 | Differences in soil structure and nutrients between perennial rice and annual rice cropping systems. **a**, Soil pH. **b**, Soil bulk density (g cm^{-3}). **c**, Soil porosity (%). **d**, Capillary porosity (%). **e**, Noncapillary porosity (%). **f**, Porosity ratio. **g**, Saturated upper limit (%). **h**, Plant available soil water capacity (%). **i**, Wilting lower limit (%). **j**, Soil organic carbon (SOC) (g kg^{-1}). **k**, Total nitrogen (TN) (g kg^{-1}). **l**, C/N ratio. Within each 10 cm increment of soil depth within each parameter, horizonal bars represent the standard error of different treatments (* $P < 0.05$; n.s., not significant). AR is annual rice. PR-2y, PR-3y and PR-4y are perennial rice in year 2, year 3 and year 4, respectively. The data are means from Experiment 3, with parameter l.s.d. being: a) 0.54; b) 0.06; c) 2.5; d) 4.6; e) 5.5; f) 0.26; g) 3.6; h) 3.4; i) 0.4; j) 1.6; k) 0.22; and l) 0.29 (N = 48; $P < 0.05$) (see Supplementary Table 9).

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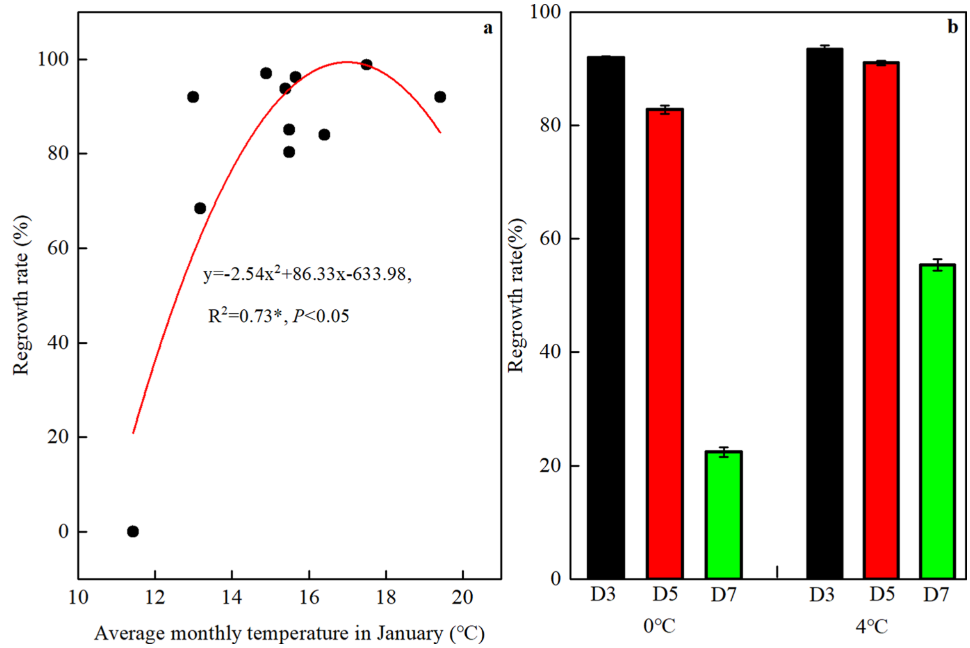

Extended Data Fig. 9 | The effect of low temperature and its duration on the regrowth of perennial rice. a, The relationship between regrowth rate of PR23 and average monthly temperature in January. The data were derived from Yuanjiang, Jinghong, Lancang, Wenshan, Simao, Yiliang, Baoshan, Yudu, Congjiang, Guizhou, Shangsi and Guanyang locations in 2016–2017. The regrowth rate of perennial rice had a significant quadratic correlation with average monthly temperature of January 2017 ($R^2 = 0.73^*$, $P < 0.05$). **b**, The effect of low temperature and its duration on regrowth rate of PR23. D3, D5 and D7 referred to the duration of low temperature condition for 3, 5 and 7 days, respectively. The error bar represents the standard error of each treatment. The data are means from Experiment 5, with l.s.d. for regrowth of a) 25.7 (N = 48) and b) 3.2 (N = 18) respectively ($P < 0.05$) (see Supplementary Tables 10 and 11).

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