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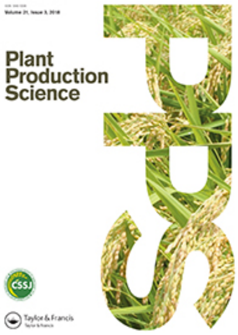

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REVIEW

Progress in varietal improvement for increasing upland rice productivity in the tropics

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ABSTRACT
Enhancing rice yield in upland rice systems through genetic improvement remains a major challenge in the tropics. This review aims to provide the trends on upland rice cultivation over the last 30 years and recent distribution of upland rice in the tropics, and to report progress in studies on genetic improvement for enhancing productivity in Africa, Asia, and Latin America. While upland rice cultivation area has reduced in Asia and Latin America over the last 30 years, the area in Africa has increased. The current share of upland rice area in total rice area is related to rainfall and gross national income per capita, especially in Africa, and higher share is associated with lower rice self-sufficiency at national level. Breeding programs in Asia and Latin America have developed high-yielding varieties using *indica* materials as parents. In Africa, New Rice for Africa (NERICA) varieties were developed from crosses between improved tropical *japonica* and *Oryza glaberrima*. However, recent studies report that there is scope for improving existing NERICA using upland *indica* materials from Asia. In highlands of Africa, there are ongoing breeding programs using *japonica* varieties, such as the Nepalese Chhomrong Dhan. Key important plant traits used in the breeding programs are not largely different across regions, especially intermediate plant height and tillering capacity (which may be related to weed-suppressive ability), and high harvest index. In conclusion, we propose an international network for breeding upland rice with accelerating seed exchange across regions that could enhance upland rice productivity through genetic improvement.

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CLASSIFICATION
Crop Physiology

1. Introduction

Rice, wheat, and maize are the world's three most important food crops. Of these, rice is the most consumed by humans, being eaten by more than half of the world's population. It provides 27% of the calories in the world's low- and middle-income countries (Dawe et al., 2010). About 900 million of the world's poor depend on rice as consumers or producers (Pandey et al., 2010).

Rice production systems can be simply classified into lowland and upland rice. In lowland rice, fields are usually flooded during part or all of the growing season; lowland rice includes rain-fed lowland, irrigated lowland, deep-water and mangrove swamp (Saito et al., 2013). Upland rice is generally grown on level or sloping, unbunded fields. Flooding is rare in this system. In some cases, especially in Latin America, supplemental irrigation may be used. Upland rice is grown under crop rotation systems with other crops, or under slash-and-burn systems (Atlin et al., 2006; Pinheiro et al., 2006; Saito, Linquist, Keobualapha, et al., 2006). Recent statistics from 71 countries from Asia, Latin America and sub-Saharan Africa show that lowland and upland rice account for 92 and 8% of total rice cultivation area, respectively, (Figure 1).

Global rice research and development efforts have largely focused on lowland rice. Together with inputs of fertilizer and irrigation, improved rice varieties have contributed to great yield increases in lowland rice throughout the world (Evans, 1993; Fischer et al., 2014; Saito, Dieng, Toure, Samodo, & Wopereis, 2015). It is generally agreed that yield is higher in lowland rice than in upland rice (Saito et al., 2017; van Oort et al., 2015), and most of future additional production will come from lowland rice to meet increasing demand (CGIAR Research Program on Rice, 2017). Nevertheless, upland rice is still important for some countries (Figure 1). The countries having lower gross national income (GNI) per capita tend to have higher share of upland rice area in total rice area (Figure 2(a))

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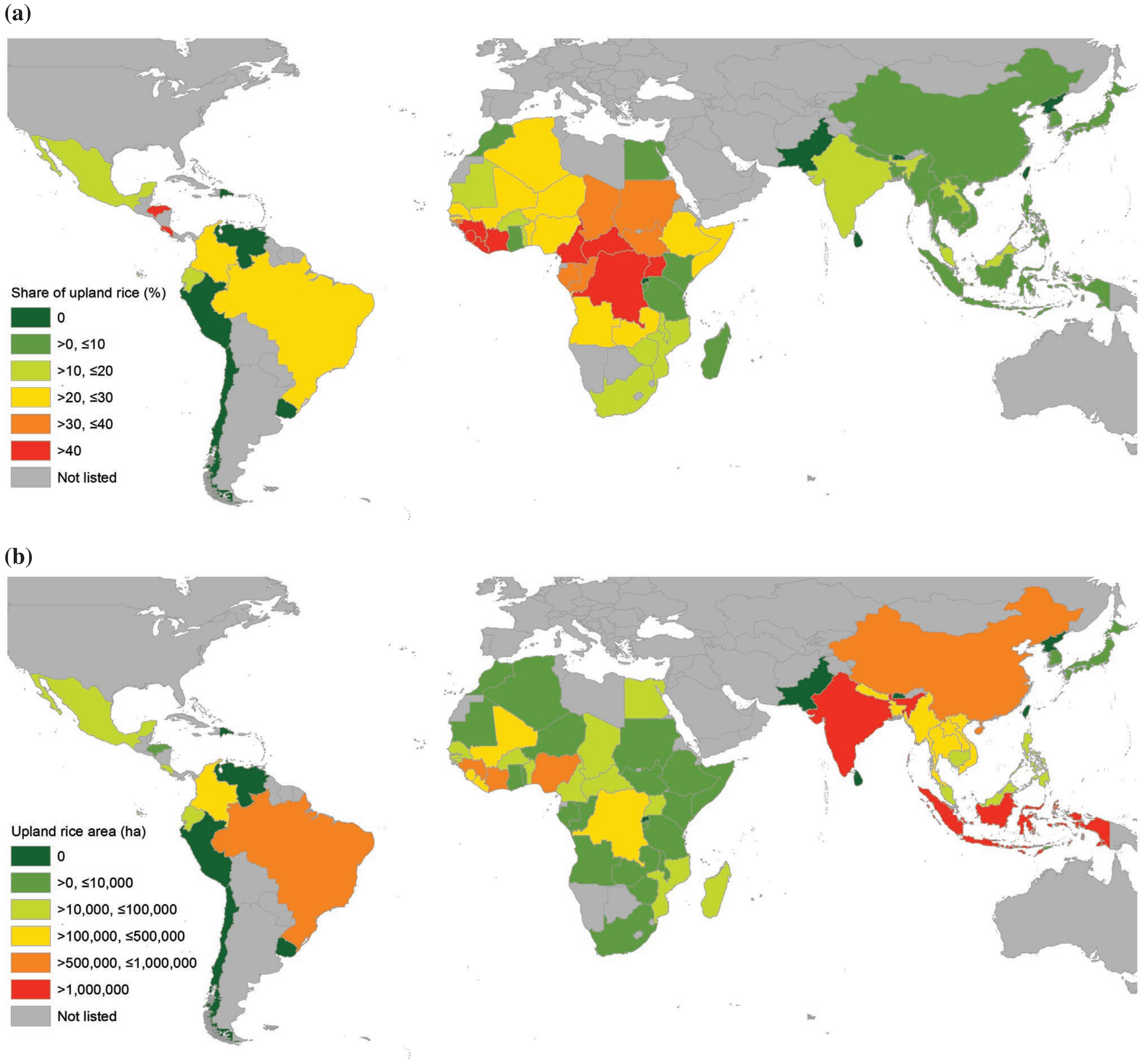

Figure 1. Spatial distribution of upland rice, as expressed in (a) share of upland rice in total rice harvested area and (b) actual upland rice harvested area at national level. Gray-colored countries are not included. Data source for Africa: Diagne et al. (2013). The predicted averages and proportions of upland rice area to total rice area were multiplied with total rice harvested area in 2009 obtained from FAOSTAT (2012). Sudan includes what is now South Sudan. Data source for Asia: IRRI strategic assessment (IRRI, 2013). Estimates of upland rice area have been combined from the best available sources for each country. Area data for each country were averaged over 2001–2010 where available and adjusted to match FAOSTAT county totals for 2008–2010. Data source for Latin America: Farmers' questionnaire investigation in 2016 (Graterol & Orrego, 2017).

and also have lower self-sufficiency for rice (production–consumption ratio; van Ittersum et al., 2016; van Oort et al., 2015) (Figure 2(b)). However, their relationships were weak. When correlation analysis was performed in each region, there were no significant relationships in Figure 2(a) and (b) (data not shown). Thus, within each region, high share of upland rice area does not mean poverty nor food insecurity.

On-farm studies in the tropics including Asia (Lao People's Democratic Republic and Vietnam) and Africa (Benin, Burkina Faso, Côte d'Ivoire, Democratic Republic of Congo, the Gambia, Ghana, Republic of Guinea, Madagascar, and Mali) have reported low yields of upland rice (less than 2 t/ha in most cases) and their causes (Affholder et al., 2013; Becker & Johnson, 2001; Saito, Linquist, Keobualapha, et al., 2006; Tanaka et al., 2017; Tsujimoto et al., 2014). In Brazil, where upland rice is predominantly grown on large mechanized farms in the cerrados, long-term statistics on upland rice yield at national level show that on-farm yield level has increased over the last 20 years, but recent yield in the late 2000s was still low, remaining around 2 t/ha (Fischer et al., 2014). Saito,

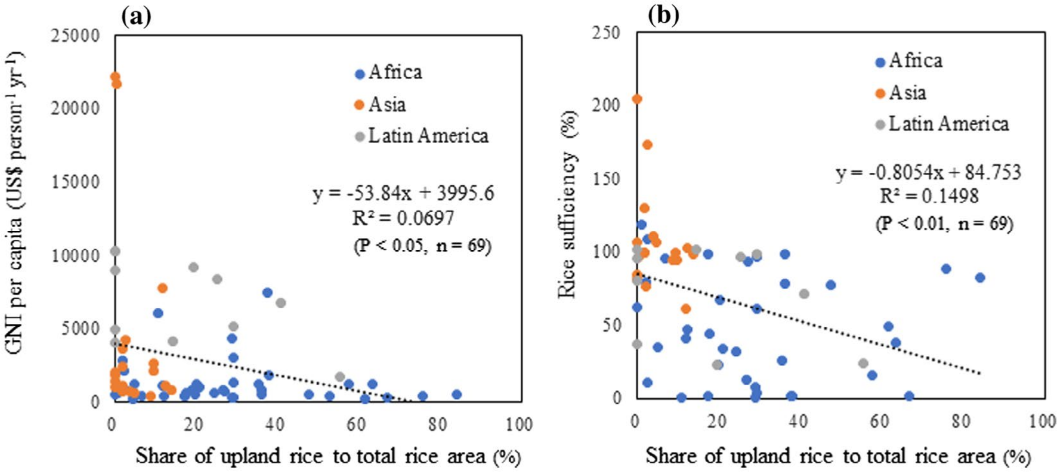

Figure 2. Relationship between share of upland rice to total rice area at national level and (a) gross national income (GNI) per capita and (b) rice sufficiency. Rice sufficiency was the ratio of domestic rice production to rice consumption. Data sources: The parameter of GNI per capita were the average over 2008–2010 from World Bank (2017). Rice self-sufficiency was based on the average over 2008–2010 from FAOSTAT (2012). Data source on share of upland rice as indicated in Figure 1. Japan and Uruguay were excluded as outliers, because of the extremely high value of GNI per capita (US$ 40,360 for Japan) and rice sufficiency (1.142% for Uruguay).

Dieng, Toure, et al. (2015) show that recent yield increases at national level are associated with share of irrigated area in total rice area in sub-Saharan Africa. This indicates that enhancing yield in rain-fed systems, including upland rice, remains a major challenge.

Low yields of upland rice are often attributed to sub-optimal crop management practices, limited availability of high-yielding varieties, and abiotic and biotic stresses (some of which might be associated with land use pressure) (Becker & Johnson, 2001; Diagne et al., 2013; Niang et al., 2017; Saito, Linquist, Keobualapha, et al., 2006; Saito et al., 2013; Tanaka et al., 2017). Typical major abiotic and biotic stresses include cold stress in highlands (Ahmadi et al., 2004; Raboin et al., 2014), drought (Kijima et al., 2011; Niang et al., 2017, 2018; Saito et al., 2013, 2017), soil-related problems including acidity and N and P deficiency (Asai et al., 2009; Haefele et al., 2014; Okada & Fischer, 2001; Saito, Linquist, Keobualapha, et al., 2006; Saito et al., 2007, 2013), weeds (Becker & Johnson, 2001; Saito et al., 2010), and soil-borne pests such as nematodes (Balasubramanian et al., 2007). There are also large year-to-year variations in abiotic and biotic stresses due to climate conditions (such as rainfall pattern), which could lead to reduced investment by farmers in inputs and result in larger yield gaps (van Oort et al., 2017). The vulnerability of upland rice production could be accelerated with global climate change (Wassmann et al., 2009). Overcoming these constraints and improving yields have been major research topics addressed through genetic improvement.

Recent breeding progress in upland rice in the tropics has replaced traditional upland rice varieties characterized by low yield, tall plants, and few tillers by improved varieties; in West Africa, the traditional varieties are often tropical *japonica* (*Oryza sativa*) or *Oryza glaberrima*, which is highly weed competitive, and resistant to local biotic and abiotic stresses (Arouna et al., 2017; Atlin et al., 2006; Futakuchi et al., 2012; Pinheiro et al., 2006; Saito & Futakuchi, 2009). However, few reports have provided an overview of progress in genetic improvement and yield gains observed for upland rice in the tropics (Gupta & O'Toole, 1986).

Therefore, the objectives of this review are to: (i) provide the trends in upland rice cultivation over last 30 years and the recent distribution of upland rice in the tropics and (ii) report progress in studies on genetic improvement for enhancing productivity. In the conclusion, we propose strategies that international researchers could adopt to improve upland rice productivity in the tropics.

This paper does not deal with drought tolerance of upland rice varieties as this has already been covered by numerous studies, review papers, and books (e.g. Bernier et al., 2007; Fischer et al., 2012; Serraj et al., 2008, 2011). In addition, we do not consider aerobic rice systems, in which rice plants are also grown in non-puddled, non-flooded conditions, but do not encounter any serious water stress because of supplemental irrigation (Kato & Katsura, 2014; Zhao et al., 2010). However, 'aerobic rice varieties' that are developed for 'aerobic rice systems' can also be used as upland rice varieties, and grown in uplands having no severe drought.

2. Trend of upland rice cultivation and its recent distribution in the tropics

Comparing data from Gupta and O'Toole (1986) with recent data shown in Figure 1 for Africa, Asia, and Latin

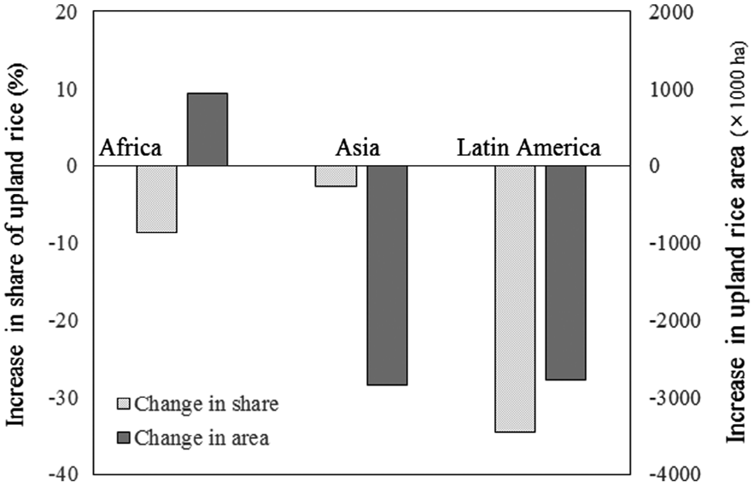

Figure 3. Change in upland rice harvested area and share of upland rice in total rice area during the past 30 years in three regions (Africa, Asia, and Latin America). Data sources: Data from Figure 1 and from Gupta and O'Toole (1986) for 1981–1982. Only those countries having data in both databases were included in this analysis. African data covers 14 countries: Benin, Côte d'Ivoire, Egypt, The Gambia, Ghana, Guinea, Guinea-Bissau, Liberia, Madagascar, Mali, Nigeria, Senegal, Sierra Leone, and Togo. Asian data covers 15 countries: Bangladesh, Bhutan, Cambodia, India, Indonesia, Lao People's Democratic Republic, Malaysia, Myanmar, Nepal, Pakistan, Philippines, South Korea, Sri Lanka, Thailand, and Vietnam. Latin American data covers 9 countries: Brazil, Colombia, Costa Rica, Ecuador, Honduras, Mexico, Republic of Dominica, and Venezuela.

America (14, 15, and 9, countries, respectively), upland rice cultivation area has been reduced by more than 2 million ha in both Asia and Latin America, whereas the area has increased by more than 1 million ha in Africa (Figure 3). In contrast, the share of upland rice in total rice area has reduced in all three regions. In Africa, the area of lowland rice cultivation also increased, and consequently the share of upland rice decreased. Dramatic reduction in upland rice area (>0.5 million ha) has occurred in India, Thailand, and Brazil, whereas Nigeria had significant increases (>0.4 million ha) (data not shown). The global trend of reduction in upland rice area could be attributed to efforts to reduce slash-and-burn agriculture, which is a farming system involving cutting and burning forest vegetation to make fields for upland crop production (van Vliet et al., 2012). Policies for establishing permanent agricultural land uses such as grass pasture and rubber plantation have been observed in regions such as Latin America (e.g. Brazil) and Southeast Asia. Such policies include land tenure security, forest conservation, land taxes, and promotion of lowland rice cultivation (Binswanger & Deininger, 1997; Padoch et al., 2007). Furthermore, this trend could be also associated with transition from traditional subsistence agriculture with few inputs to intensified systems for upland rice cultivation, as the production needs to be increased within smaller areas, unless there is any possibility to expand lowland area. In Brazil, the rice cultivation area has been shifted to less risky savannah areas, where farmers adopted modern technologies (Pinheiro et al., 2006); consequently, the reduction in production did not follow the trend of upland rice area. In mountainous regions of southern China, upland rice is grown on non-flooded terraces under intensive management, replacing the traditional upland rice-based slash-and-burn systems (Atlin et al., 2006). In mountainous area of Lao People's Democratic Republic (PDR), use of inputs such as herbicides has been rapidly adopted by smallholder farmers (Asai et al., 2017). The success of such a transition requires new varieties adapted to intensified upland rice systems (Atlin et al., 2006; Dingkuhn et al., 2006; Pinheiro et al., 2006).

Recent statistics have shown that Asia, Latin America, and sub-Saharan Africa accounted for 65, 10, and 25% of total upland rice area across 71 countries, which is equivalent to 8.8, 1.2, and 3.2 million ha respectively (Figure 1). Upland rice accounted for 6, 19, and 32% of total rice area in Asia, Latin America, and Africa, respectively. In Asia, there was no more than 10% of upland rice in most countries. Coastal West and Central African countries had larger shares of upland rice area. These countries tended to have higher rainfall (>1500 mm), and belong to tropical-warm/humid zone (Saito, Dieng, Toure, et al. 2015). In Latin America, Costa Rica and Honduras had the largest shares of upland rice. There was more than 1 million ha of upland rice cultivation in India and Indonesia (6.0 and 1.2 million ha, respectively). Brazil had the third largest upland rice area among the 71 countries (0.9 million ha), followed by three African countries – Côte d'Ivoire, Nigeria, and Guinea.

Following Tanaka et al. (2015), we performed classification and regression tree (CART) using region (three regions as mentioned above), national rainfall index (as

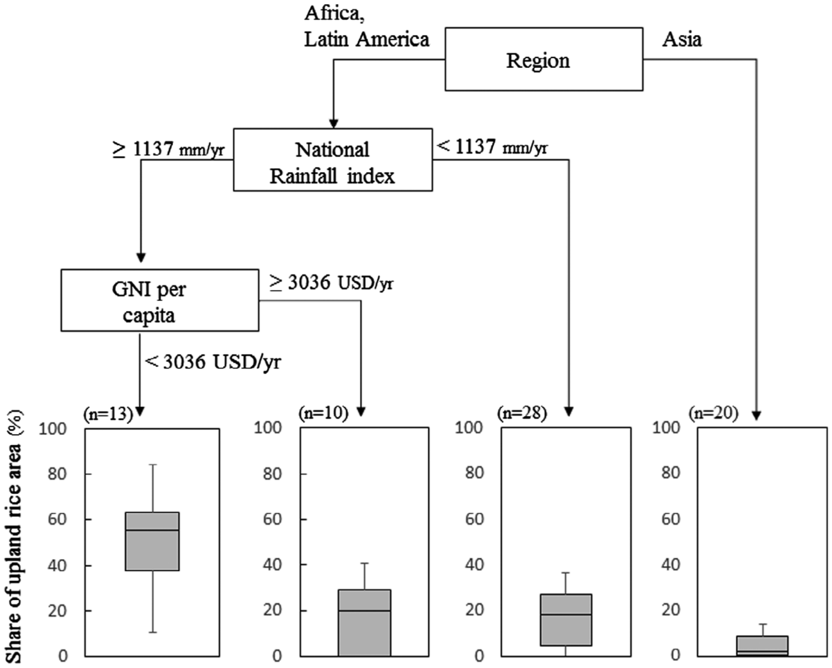

Figure 4. Regression tree analysis explaining variation in share of upland rice area in total rice area at national level.
The analysis was performed with rcart library of R software. The predictor parameters tested included a categorical variable of 'region' and quantitative variables of 'rice consumption amount per capita', 'population density per land area', 'net amount of rice import (= export − import)', 'GNI per capita', and 'national rainfall index'. The data on GNI per capita and national rainfall index are from the database of World Bank (2017) and AQUASTAT (2017), respectively, and the others from FAOSTAT (2012) . Each parameter was the average over 2008–2010, except for national rainfall index obtained from the data of 2002.

an indicator of the precipitation quality of the agricultural season), GNI per capita, and population density for explaining variation in share of upland rice. This analysis found that the primary factor was region (Figure 4): Latin America and Africa were in the same group, and tended to have larger share of upland rice. This group was further divided by national rainfall index. In the group with higher national rainfall index (≥1137 mm/year), share of upland rice is higher in countries with low GNI per capita (<3036 USD/year). The group consists of 13 countries – Cameroon, Central African Republic, Côte d'Ivoire, Democratic Republic of Congo, Guinea, Guinea-Bissau, Liberia, Madagascar, Nigeria, Republic of Congo, Sierra Leone, and Uganda from Africa, and Honduras from Latin America. Another group having higher GNI comprised six Latin American and four African countries. The group with lower national rainfall indices (<1137 mm/year) comprised 2 Latin American and 26 African countries. These results confirm the importance of rainfall for upland rice cultivation, its cultivation in relation to poverty, and historical differences in rice cultivation between Asia and other regions.

3. Breeding efforts and genetic gains in the tropics

In this section, we describe research on genetic improvement in the three regions, Asia, Latin America, and sub-Saharan Africa. We do not cover all the countries, but focus on a few countries in each region, where progress in research has been reported internationally. Furthermore, we did not include India and its research on improvement of drought tolerance (Mandal et al., 2010; Sinha et al., 2009).

3.1. Asia

In Asia, the International Rice Research Institute (IRRI) has played important roles in the development and distribution of improved upland rice varieties (Atlin et al., 2006; Lafitte et al., 2002), as it has for lowland rice varieties. It is noted that Upland Rice Research Consortium was established in 1991, and enhanced collaboration between national agricultural research institutes in Asia and IRRI (Piggin et al., 1996). Furthermore, the International Network for Genetic Evaluation of Rice (INGER) has enabled to exchange and evaluate promising varieties and elite breeding materials (for detailed information, see http://inger.irri.org). In this sub-section, we review cases from China, Indonesia, Lao PDR, and the Philippines.

Yunnan Province in southern China is located in humid sub-tropical zone. The trends in breeding are similar to other countries in the Asian tropics and Yunnan has made some advanced progress. The upland rice breeding program that was initiated in the early 1980s led to the release of Yunlu 29, Yunlu 52, Luyin 46 (B6144F-MR-6-0-0 from Indonesia) and Siluxuan 6 (Tao et al., 2009). These varieties are well adapted to high-input intensified systems, and can reach yields of 4 t/ha, while traditional upland varieties produce only 2 t/ha (Atlin et al., 2006; Tao et al., 2009). The yield advantage of the improved cultivars results mainly from the significant increase in tillering ability and panicle size. Adoption rate of these improved high-yielding upland rice varieties increased from 25% in 2000 to 35% in 2004 (Wang, 2006), and further to 50% in 2011 (Yunnan Science & Technology Department, 2014) across Yunnan Province. The increased adoption of improved upland rice varieties concurred with shifting from cultivation on slopes to more on terraces, from low to high inputs, and from monoculture to intercropping with maize (Wang, 2006; Yunnan Science & Technology Department, 2014). The Yunnan case shows that the adoption of improved varieties together with improved practices is an entry point that can effectively help farmers break out of the vicious circle of low productivity–poverty–environmental degradation that characterizes upland rice-based systems in Asia (Wang et al., 2010). Since 2002, upland rice breeding program in Yunnan has shifted from targeting at sloping uplands to favorable uplands with good management, developing varieties with high yield, blast resistance, and fine grain quality (Tao et al., 2009). A new generation of upland rice varieties suitable for favorable uplands such as Yunlu 101, Yunlu 103, Yunlu 140, and Yunlu 142 were released for cultivation in Yunnan in 2010–2016 (Tao Dayun, personal communication, 22 December 2017) (Table 1).

Table 1. A list of selected varieties which were recently released in selected countries.

Designation/parentage	Variety name	Country	Year
Asia			
Teqing/BG300	Yunlu 101	China	2010
WAB450-24-3-P33-HB/WAB-24-2-5-P4-HB	Yunlu 103	China	2013
Dianjingyou 1/B6144F-MR-6	Yunlu 140	China	2014
Yundao 1/Acc.104613//Yundao 1	Yunlu 142	China	2016
IR 74371-54-1-1	Sahod Ulan 1	Philippines	2009
IR 79913-B-176-B-4	Katihan 1	Philippines	2011
IR 82635-B-B-47-2	Katihan 2	Philippines	2014
IR 86857-101-2-1-3	Katihan 3	Philippines	2014
B6144F-MR-6-0-0	Hardinath 2	Nepal	2010
IR 74371-70-1-1	Sukha Dhan 3	Nepal	2010
IR 74371-46-1-1	Sukha Dhan 1	Nepal	2011
IR 74371-54-1-1	Sukha Dhan 2	Nepal	2011
IR 79971-B-191-B-B	Inpago LIPI Go 1	Indonesia	2011
IR 79971-B-227-B-B	Inpago LIPI Go 2	Indonesia	2011
IR 79971-B-102-B-B	Inpago LIPI Go 4	Indonesia	2014
Latin America			
CT11891-2-2-7-M	CORPOICA Llanura 11	Colombia	2011
PCT11:Bo:1:1>1-M-89-2-1-M-M	Yara	Bolivia	2009
PCT11:Bo:1:1>1-M-53-1-1-M-M	Paya	Bolivia	2009
CNAx7100-B-13-M1-M1-3	BRS Esmeralda	Brazil	2013
Sub-Saharan Africa			
ART3-11L1P1-B-B-2	ARICA 4	Uganda	2013
WAB95-B-B-40-HB	ARICA 5	Uganda	2013
WAB95-B-B-40-HB	ARICA 5	Guinea	2014
CNAX 3031-78-2-1-1	ARICA 16	Benin	2013
CNAX 3031-78-2-1-1	ARICA 16	Mali	2016
SCRiD 6-3-2-3-2-5	FOFIFA 173	Madagascar	2012
SCRiD186-32-2-4-4-5	FOFIFA 180	Madagascar	2014
SCRiD 198-15-2-2-4-4	FOFIFA 181	Madagascar	2014
SCRiD 91-10-1-3-2-5	FOFIFA 182	Madagascar	2014
SCRiD111-1-4-3-3-5	FOFIFA 185	Madagascar	2015
SCRiD185-26-1-5-3-5	FOFIFA 186	Madagascar	2015

In IRRI, the Philippines, Lafitte et al. (2002) show that upland rice yield has been improved through traditional breeding approaches in both unfavorable and favorable conditions in terms of soil fertility and water conditions. Improved upland *indica* varieties such as IR 55423-01 (Apo) that have intermediate plant height and number of panicles, strong weed-suppressive ability, and can maintain harvest index under water deficit conditions during reproductive stage (one of the traits for drought tolerance), have been developed (Atlin et al., 2006; Lafitte et al., 2002). Apart from IRRI breeding materials, B6144F-MR-6-0-0 was also identified as high yielding with strong weed-suppressive ability (Zhao et al., 2006). Zhao et al. (2010) report progress in the development of new breeding materials that outyielded Apo by 10%. Seven of these new breeding materials have been officially released as upland varieties in Bangladesh, India, Indonesia, Nepal, and Philippines since 2009 (Zhao & Kumar, 2016) (Table 1). Zhao and Kumar (2016) summarize the following important traits to work on in IRRI's varietal improvement program: grain yield, plant height (intermediate plant type: 100–120 cm), crop duration (short to medium growth duration: 100–115 days), lodging resistance, drought tolerance, weed-suppressive ability, resistance of diseases (blast and bacterial blight). In the practice of varietal development at IRRI, screening protocols were also developed or refined and have been used for effective breeding (Atlin et al., 2006; Zhao et al., 2006, 2010). One example is to use two-stress-level to screen for yield and drought tolerance in field (Zhao et al., 2010). Another is indirect selection criteria for weed competitiveness, which include early vegetative vigor and yield under weed-free conditions (Zhao et al., 2006). Disease resistance was firstly screened in 'disease nurseries' at F_2 and then in main field at later generations (Zhao et al., 2016). Recently, IRRI incorporated grain quality into its screening protocol to improve the market acceptability of upland rice varieties, and also looked into root-knot nematode tolerance (Zhao & Kumar, 2016).

In northern Lao PDR, where low-yielding traditional upland rice varieties were grown under slash-and-burn systems (Saito, Linquist, Atlin, et al., 2006), improved *indica* varieties Apo and B6144F-MR-6-0-0 showed better yield performance in both non-fertilized and fertilized conditions than local traditional varieties (Asai et al., 2009; Asai & Soisouvanh, 2017; Saito, Linquist, Atlin, et al., 2006; Saito et al., 2007). B6144F-MR-6-0-0 has better ability to recover from weed competition at early vegetative stage than Apo (Saito et al., 2010). Furthermore, it was reported that B6144F-MR-6-0-0 produced 4.8 t/ha of grain, two folds of yield of the local check (2.2 t/ha), in a demonstration of rice-maize intercropping in the Oudomxai Province in 2011 (Chen, 2011). Although Apo and B6144F-MR-6-0-0 showed great yield advantage over local traditional varieties, they have not been broadly adopted in northern Lao PDR, due to consumers' preference for glutinous rice. Besides outstanding yield in northern Lao PDR, good performance of B6144F-MR-6-0-0 was also reported in India, Nepal (Mandal et al., 2016; Yadaw et al., 2016), and Vietnam. This variety was released in Nepal in 2010 (Table 1), and in Vietnam in 2017 (Tao Dayun, personal communication, 22 December 2017).

In Indonesia, several improved varieties have been released with major improvements in yield, maturity, blast resistance, and tolerance of aluminum toxicity and drought in recent years (Lubis & Kustiano, 2009). These include Situ Bagendit, released in 2002. Chin et al. (2011) report that introgression of the major quantitative trait locus (QTL) *Phosphorus uptake1* (*Pup1*) into this variety, in which this locus is naturally absent, has the potential to significantly improve plant performance. *Pup1* confers tolerance of soil phosphorus deficiency. Additionally, three improved varieties derived from the cross Vandana × Way Rarem in IRRI were released in Indonesia in 2011–2014 (Zhao et al., 2016) (Table 1). This is an example of success of empirical breeding in combining high yield with drought tolerance (Bernier et al., 2007).

3.2. Latin America

Martinez et al. (2014) review rice breeding activities in Latin America, and report on the upland rice breeding programs at the International Center for Tropical Agriculture (CIAT) and in Brazil. CIAT and Centre de coopération internationale en recherche agronomique pour le développement (CIRAD) have contributed to upland rice breeding in Latin America through distribution of breeding materials or populations (*indica*, tropical *japonica*, and *indica* × tropical *japonica* materials) to national agricultural research institutes and their capacity development. These institutes have focused on population breeding scheme whereby a population composed of various upland varieties from Africa, Asia, and Latin America was improved through successive cycles of recurrent selection (Breseghello et al., 2011; Guimarães, 2005; Martinez et al., 2014). The materials developed by those institutes have been used by national partners to develop their own genetically enhanced germplasm (Guimarães, 2005). Historically, the upland rice breeding program has focused on highly productive, blast-resistant, short-cycle rice, mainly of tropical japonica type with specific adaptation to acid soils such as cerrados of Brazil and savannas of Colombia. In 1980s to early 1990s CIAT successfully developed two varieties for the savanna condition of Colombia, Oryzica sabana 6 and Oryzica sabana 10, released in 1991 and 1995, respectively. Both varieties were characterized with high tolerance to acid soils and aluminum toxicity and yield ranging from 2.9 to 3.6 t/ha. In 1990s, in collaboration with CIRAD, CIAT developed new genetic materials with focus on widening the genetic basis of the germplasm used in upland rice breeding program. As a result, CORPOICA Llanura 11 was released in Colombia in 2011 by the national partner Corporación Colombiana de Investigación Agropecuaria (CORPOICA) for the savannah agroecosystem, with high potential yield (4.6 t/ha), short cycle (105 days to harvest), disease resistance, and a good grain quality that particularly fits industrial uses. A large number of lines extracted from populations managed through recurrent selection were distributed to various national programs and exploited to include as parental lines in breeding programs, or to develop genetically advanced and highly performing lines. As a result, two upland rice composite populations, PCT4 and PCT11 gave rise to three varieties, Esperanza, Yara, and Paya released for the upland conditions in Bolivia (Martinez et al., 2014). Various candidate lines, extracted from upland rice composite populations developed and improved for adaptation to acid soil conditions (pH ~ 4 and with >70% aluminum saturation) and blast resistance (Châtel et al., 2008), are currently under testing for release in Colombia, Bolivia, and Nicaragua. Additionally, in the early 2000s, CIAT–CIRAD engaged on research projects on participatory breeding of upland rice focused on small and medium scale famers (Trouche et al., 2006). While these activities allowed identifying candidate lines for varietal release in the certain regions, they also highlighted the complexity and the need to adapt breeding objectives to the diversity of farmers' expectation in terms of new varieties. More recently, the CIAT–CIRAD upland rice breeding program is optimizing its breeding pipeline by including model-assisted multi-trait phenotyping approaches (Rebolledo et al., 2013), crop models (Rebolledo et al., 2015), and genomic prediction (Grenier et al., 2015) to accelerate genetic gain in upland rice breeding.

In Brazil, where landraces of upland rice are tropical *japonica* types that are often tall and susceptible to lodging, and have bold grains with low amylose content (Pinheiro et al., 2006), Guimarães (2002) reports historical genetic diversity and improvement, including material exchanges. Since the 1990s, introduction of materials from CIAT and the United States has accelerated progress in breeding for high-yielding ability and grain quality (Breseghello et al., 2011), as Brazilian consumers prefer the slender and high-amylose content of lowland rice (*indica* type). CIAT upland materials, although based on a *japonica* background, have some introgression from *indica*. Materials from the United States have good grain quality, which is required to ensure competitiveness in terms of market price against irrigated rice from southern Brazil and to increase the profitability of upland rice cultivation. Furthermore, since 1990s, the breeding program has focused on high-input, fully mechanized cropping systems, primarily targeting favorable production zones, in which grain appearance, yield potential, blast resistance, and lodging resistance are prioritized. Major breeding achievements were the development of BRS Premavaila with grain quality competitive against lowland rice, and CN8555 with wide environment adaptability. Direct grain-yield selection has been targeted primarily to the most favorable conditions, and showed significant genetic yield gain over 25 years (Breseghello et al., 2011). Over this period, there was a shortening in time to flowering and plant height (0.25 days/year and 0.52 cm/year, respectively). Key plant types are intermediate plant height (90–100 cm), abundant and upright tillering ability (200–250 tillers/m^2), and resistance to lodging and competitiveness against weeds and grass (*Brachiaria*) under rice-pasture rotations (Pinheiro et al., 2006). Recent studies have shown the importance of genotype × environment interaction, and propose new breeding approaches that take into account drought-stress patterns (Heinemann et al., 2008, 2015).

3.3. Sub-Saharan Africa

One famous achievement in genetic improvement in upland rice in sub-Saharan Africa over the last 30 years is development and diffusion of New Rice for Africa (NERICA) (Dingkuhn et al., 2006; Saito et al., 2012; Tollens et al., 2013). In the 1990s, the Africa Rice Center (AfricaRice; then known as the West Africa Rice Development Association [WARDA]) initiated the development of interspecific varieties from the wide cross between improved tropical *japonica* and *O. glaberrima*. Some 18 good-performing varieties derived from these crosses were named as NERICA 1 to NERICA 18. Many studies have shown the wide adaptation of NERICA varieties and their impact on farmers' livelihoods in sub-Saharan Africa (e.g. Arouna et al., 2017; Kijima et al., 2008, 2011; Yokouchi & Saito, 2016, 2017). Diagne et al. (2015) reported rice area planted to NERICA varieties at national level in 13 countries. Based on available data at that time (e.g. Saito et al., 2010; Saito & Futakuchi, 2009; Touré et al., 2011), Saito et al. (2012) argued that, in comparison with their parents, NERICA varieties did not have superior yielding ability in harsh environments characterized by (e.g.) poor soil fertility and heavy weed infestation. Since the publication of that paper, there have been many reports supporting this argument in West Africa (Saito, 2014, 2016; Saito & Futakuchi, 2014; Sito, Dieng, Vandamme, et al., 2015; Saito, Vandamme, Segda, et al., 2015; Saito et al., 2014; Vandamme et al., 2016a; Vandamme et al., 2016b). In East and Southern Africa, good performance of upland NERICA varieties has been frequently observed in field trials and on farm (Kijima et al., 2008; Sekiya et al., 2013; Shrestha et al., 2012). The reasons for differences in performance of upland NERICA varieties between sub-regions are not well known. However, they may be related to soil fertility and water conditions. Some NERICA varieties show good performance under drought conditions in West Africa (Dr K. Futakuchi, personal communication, 23 August 2017). Higher yield response to fertilizer has also been observed in NERICA 1 (Saito & Futakuchi, 2009). Recently, new high-performing upland rice varieties were identified and nominated as Advanced Rice Varieties for Africa (ARICA), based on results from multi-locational trials through 'Africa-wide Breeding Task Force' led by AfricaRice (Table 1). The Breeding Task Force comprises international and national rice breeders from more than 30 African countries. Up to now, three upland ARICA varieties have been officially released in four countries (Table 1).

Exploring new donors and development of efficient and high-throughput phenotyping protocols have been initiated to develop new rice varieties beyond NERICA at AfricaRice. Similar to results from Asia (Asai et al., 2009; Atlin et al., 2006; Saito et al., 2007), Saito and Futakuchi (2009), Saito et al. (2012, 2014) identified B6144-F-MR-6-0-0 (an *indica* variety developed in Indonesia) as a potential donor for improving yield under low-input conditions. Aus257 was identified as early maturing and high yielding, with strong weed-suppressive ability and greater nutrient uptake than NERICA 1 (Saito, 2016; Saito & Futakuchi, 2014). IR 74371-3-1-1 (an *indica* variety developed in the Philippines) showed higher nutrient-use efficiency than NERICA 1, which contributed to higher yield in low-input conditions (Saito, 2016). Recently, DJ123 was also identified as a potential donor for tolerance to soil P deficiency and good responsiveness to P fertilizer application (Vandamme et al., 2016b, 2018). Growth and yield performance of CG14 (*O. glaberrima*) under low-input conditions, including low P conditions, was also confirmed (Saito & Futakuchi, 2009; authors' unpublished data). Currently, identification of a QTL conferring an adaptation mechanism to low soil fertility conditions is ongoing. Obara et al. (2010) identified a QTL that promotes root elongation under N-deficient conditions. That QTL was from Kasalath, which is well-known material. Aus257, DJ123, and Kasalath are *indica* type, belonging to the *aus* group of varieties, which are very early maturing, drought

Table 2. Desirable traits for developing the superior upland rice varieties in the tropics.

	Country	Early vigor	Weed suppressive ability	Lodging resistance	Harvest index	Biomass accumulation	Maturity	Plant height	Tillering ability	Grain quality
Asia										
Atlin et al. (2006)	Philippines	✓	✓		✓			✓	✓	
Saito, Linquist, Atlin, et al. (2006)	Lao PDR				✓	✓		✓	✓	
Saito et al. (2007)	Lao PDR				✓	✓		✓	✓	
Asai et al. (2009)	Lao PDR				✓				✓	
Lubis and Kustiano (2009)	Indonesia						✓			✓
Tao et al. (2009)	China				✓			✓	✓	
Zhao et al. (2010)	Philippines	✓			✓					
Asai and Soisouvanh (2017)	Lao PDR			✓	✓		✓	✓	✓	
Latin America										
Pinheiro et al. (2006)	Brazil		✓	✓				✓	✓	✓
Breseghello et al. (2011)	Brazil			✓			✓	✓		✓
Sub-Saharan Africa										
Saito and Futakuchi (2009)	Benin	✓	✓		✓	✓			✓	
Saito et al. (2012)	Benin	✓	✓		✓	✓		✓	✓	
Raboin et al. (2014)	Madagascar	✓	✓		✓		✓			
Saito (2016)	Benin	✓	✓		✓	✓	✓		✓	

*Tolerance/resistance to abiotic and biotic stresses and input-responsiveness were not included in this table.

tolerant, and grown under upland conditions in Bangladesh and West Bengal state of India (Khush, 1997). *Aus* genotypes could be useful genetic resource for Africa as well. Several protocols have recently been developed to improve screening (Saito, 2010, 2014; Sito, Dieng, Vandamme, et al., 2015, Saito, Vandamme, Segda, et al., 2015; Vandamme et al., 2016b), and plant types required for high yield proposed (Saito, 2016; Saito & Futakuchi, 2009).

In the highlands of Madagascar, CIRAD and Centre National de Recherche Appliquée au Développement Rural (FOFIFA) initiated breeding programs in the 1980s to introduce upland rice cultivation where the development of new lowland fields was not possible and there was no upland rice cultivation due to a lack of rice varieties adapted to cold conditions. Ahmadi et al. (2004) report on initial efforts in the breeding program, and achievements to the early 2000s. Raboin et al. (2010) report that materials developed in Madagascar had also been tested in the highland areas of the Andes in Bolivia and Colombia, Latin America. The collaborative efforts resulted in official release of Nepalese irrigated-lowland *japonica* variety Chhomrong Dhan in 2006 in Madagascar (Raboin et al., 2013, 2014). This variety clearly showed yield advantage over varieties released in the 1990s and 2000s in field trials (Raboin et al., 2014), and its higher yield was attributed to higher leaf area index, high harvest index, and long duration; it also has weed-suppressive ability. Chhomrong Dhan now accounts for more than 80% of upland rice area in Madagascar, and has been used as donor in recent breeding. Among the six varieties releases in Madagascar shown in Table 1, except for FOFIFA 185 are derivatives of Chhomrong Dhan. Chhomrong Dhan was also released in Rwanda, where cold is a major constraint.

4. Synthesis and conclusions

In Asia and Latin America, progress in upland rice breeding has been made through the use of *indica* materials as donors. In Africa, tropical *japonica* and *O. glaberrima* have been major donors for upland rice breeding (e.g. development of NERICA varieties adapted not only to West Africa but also to East and Southern Africa). However, recent studies have clearly shown that the use of *indica* materials could enhance upland rice productivity in Africa.

For cold-prone environments such as the highlands of Madagascar, cold-tolerant Asian materials could also play an important role as shown in the case of Chhomrong Dhan. Such cold-tolerant materials could also be tested in the highlands of Latin America. The cases of Chhomrong Dhan, B6144F-MR-6-0-0, and NERICA varieties indicate that broad adaptation across regions in the tropics is possible, and enhancing exchange of germplasm would accelerate progress in genetic improvement.

Therefore, we argue for the establishment of an international network for testing of newly developed breeding materials or populations beyond the existing networks in each region (International Network for Genetic Evaluation of Rice for IRRI's target countries mainly in Asia; Fondo Latinoamericano para Arroz de Riego (FLAR) in Latin America; Africa-wide Rice Breeding Task Force in Africa). Within the framework of CGIAR, the CGIAR Research Program on Rice (RICE) was initiated in 2017 (CGIAR Research Program on Rice, 2017). An international germplasm-exchange network will be established as part of RICE's 'flagship project'. Although the current proposal seems to largely target irrigated and rainfed lowland rice, it is desirable that a sub-network for upland rice be established.

Table 2 shows desirable characteristics for developing high-yielding upland rice varieties in different studies across three regions discussed in this review paper. Harvest index, plant height, and tillering ability are predominantly reported as key types. Intermediate height, intermediate number of tillers, and high harvest index have been proposed in most cases. Apart from these, early vigor and weed-suppressive ability are also important, and can be related to plant height and tillering capacity. Grain quality was not addressed in most upland breeding programs in early ages except that for Latin America and Indonesia. Generally, grain quality required for the majority of the markets in Latin America are long slender non-sticky grain with high amylose content. In recent years, grain quality has been seriously considered in most upland breeding programs in Asia and Africa. At IRRI, for example, low chalkiness (<10%) and high head rice (>50%) are strictly screened for; other quality traits such as grain shape, amylose content, gelatinization temperature, and gel consistency, are selected for based on preferences of a target region (Zhao & Kumar, 2016). Although we do not include input responsiveness, drought tolerance, or resistance to other abiotic and biotic stresses in Table 2, they are also important traits to be considered.

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