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# Stability and yield performance of genotypes: A proposal for regrouping world rice area into mega-environments

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**Rice ecosystems are characterized by elevation, rainfall pattern, depth of flooding and drainage, and by the adaptation of rice to these agroecological factors. Many divisions were made in the attempts at defining and identifying specific ecosystems and their breeding objectives. Genotypes are evaluated every year in multilocational trials. The aim was to study the performance of breeding lines developed for various ecosystems and to identify stable genotypes with wide adaptability. The data from 1341 all-India coordinated experiments (1970–94), and 1305 international experiments (1975–94) on the performance of rice cultivars were used. Mean yield, coefficient of variation and regression analyses identified several cultivars, developed at different centres, as stable for yield. These genotypes, with varying genetic makeup that crossed geographic boundaries and spread over ecosystems based on their sensitivity or insensitivity to photoperiod and maturity duration, are identified as universal genotypes for a specific mega-environment. They differ in the genetic expression of maturity period and photosensitivity. The diversity in these genotypes has successfully prevented vulnerability and yield instability in mega-environments. In this study, no genotype was found to significantly surpass the grain yield of 10 t/ha, established by the photoinsensitive universal genotypes, IR 8 and Jaya with medium maturity period, developed in 1966 and 1968, respectively. The singular reason for this dismal performance is the plethora of breeding objectives assumed essential for the targeted ecosystems. We, therefore, suggest a regrouping of rice habitats into four mega-environments: (1) rainfed unfavourable uplands requiring varieties with photoinsensitivity and very early maturity (< 90 days); (2) rainfed favourable uplands and irrigated areas requiring varieties with photoinsensitivity and early maturity (90–110 days); (3) irrigated areas requiring varieties with photoinsensitivity and medium maturity (120–135 days); and (4) rainfed lowlands requiring varieties with photosensitivity or insensitivity and late maturity (> 140 days). This delineation can motivate rice breeders to push yields of universal genotypes beyond the 10 t/ha barrier.**

RICE (*Oryza sativa* L.) is produced over a wide range of locations and climatic conditions. The bulk of rice area

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is subjected to an alternating wet and dry seasonal cycle, and contains many of the world's major rivers, each with its own vast delta. Here enormous flat, low-lying agricultural lands are inundated and flooded annually during the crop-growing wet season. Only rice adapts readily to production under these conditions of humid air, saturated soil and high temperatures.

After the introduction and spread of high-yielding semidwarf cultivars, rice culture was classified according to the source of water supply as rainfed or irrigated[1]. The rainfed class was further categorized into rainfed upland and rainfed lowland. Then, depending on water regimes, rice land was classified as upland with no standing water, lowland with 5–50 cm of standing water, and deep water with > 50 cm to 5–6 m of standing water. Buddenhagen[2] classified rice culture in West Africa as upland (either dryland or hydromorphic), irrigated, inland swamps and flooded (riverine shallow, deep, or mangrove). Rice lands in South and South-east Asia were grouped[3] as irrigated, rainfed uplands and rainfed lowlands with shallow rainfed (5–15 cm), intermediate deep rainfed (16–50 cm), semideep rainfed (51–100 cm) and deep water (> 100 cm). De Datta[4] suggested that deep water and floating rice areas that are direct-seeded into dry soil be excluded in this classification from the rainfed lowland transplanted rice area. Huke[5] analysed 30 m ha of shallow rainfed lowlands; medium-deep rice lands were not included, since maps did not separate these areas from deep-water rice lands.

A major review of these systems throughout the world was undertaken by an international committee[6]. This committee proposed for international usage, 18 distinct categories of rice lands subdivided into five broad classes: (i) irrigated – with favourable temperature, low temperature tropical and low temperature temperate; (ii) rainfed shallow – favourable, drought-prone, both drought and submergence-prone, submergence-prone and rainfed medium-deep waterlogged; (iii) deep water (50–100 cm) and very deep water (> 100 cm); (iv) upland – favourable with long growing season, favourable with short growing season, unfavourable with long growing season and unfavourable with short growing season; and (v) tidal wetlands – with perennial freshwater, seasonal or perennial saline water, acid sulphate soils and peat soils. Accordingly, Khush[6] discussed the attributes of these systems and suggested general methods for breeding improved materials.

Over 60 scientists engaged in rainfed lowland rice improvement identified four categories of rainfed lowland rice: rainfed shallow drought-prone, rainfed shallow drought and submergence-prone, rainfed shallow submergence-prone and rainfed medium-deep waterlogged[7]. However, the need for better data on the relative importance and spatial distribution of the lands in several classes of rainfed lowland was recognized. Weather and climate determinants have been used for resolving rice ecosystems. Oldeman *et al.*[8] perceived four groups of rice-growing regions as highly seasonal, moderately seasonal, weakly seasonal and non-seasonal, based on the seasonal fluctuations in mean monthly minimum temperature. New computer simulation techniques and geographic information systems were used to analyse further the determinants, including climate changes of a range of environments[9].

The major objectives of rice-breeding programmes include yield stability, lodging resistance, fertilizer responsiveness and pest resistance. Forty other plant characters (traits) were also included[3] later, to suit the varied system of classification of rice ecosystems and their assumed needs. In rainfed lowlands, photosensitive cultivars dominate. In some areas, however, photoinsensitive cultivars can also be grown if information is available on the cessation of monsoon. Adaptation advantages make farmers in rainfed lowland prefer photosensitive cultivars in shallow to deep-water areas. In photosensitive cultivars, the maturity period is fixed by day length, regardless of planting date. Photosensitivity functions as a safety mechanism, when the onset of monsoon is considerably delayed. The sensitivity of cultivars to photoperiod is usually classified[10] as strongly sensitive, weakly sensitive, essentially insensitive and insensitive.

Early generation high-yielding cultivars like IR 8 and Jaya were selected, not only for high-yielding ability but also for wide adaptability, making it possible to use the same cultivars over broad geographical areas. However, farmers are more concerned with the risk involved in any new technology and are more interested in the yield stability over time. One of the most important causes of yield instability in non-irrigated agriculture is unreliable rainfall, resulting in drought or excess moisture[11], or limited availability of solar radiation[12] during crop growth. Hence, yield stability within broad ecosystems must be given priority. Every year rice genotypes are pooled and tested over a wide range of environments. The objective was to study in these experiments, the performance of high-yielding breeding lines developed for various ecosystems and to find stable rice genotypes with wide adaptability.

The first and the largest national multilocation testing programme was initiated in 1965 under the All India Coordinated Rice Improvement Project, now known as the Directorate of Rice Research[13]. As rice improvement was considered essential for meeting basic food requirements of the world population, similar experiments were initiated in 1975 at the international level[14]. We used the data on the performance of cultivars from all-India coordinated experiments organized by the Directorate of Rice Research, Hyderabad, India and from similar trials conducted by the International Rice Research Institute, Philippines. Data sets from 2646 experiments, 1341 all-India coordinated experiments and 1305 of the International Rice Testing Programme trials, were analysed. The all-India coordinated experiments were performed from 1970 to 1994 at 53 locations in 16 states in India. The maturity period of the test entries was considered for inclusion in these experiments for evaluation at multilocations in major ecosystems, rainfed lowland, semideep–deep water, irrigated and upland. The locations in the international experiments conducted during 1975–93 were well distributed geographically in 51 countries, ranging from latitude 35°N to 30°S, longitude 160°E to 109°W, and altitude 1 to 1500 m above mean sea level. About 35% of these trials was in East and South-east Asia, 30% in South Asia, 25% in West Asia and 10% in Latin America. The number of countries and location within any particular country or areas, varied in these experiments. The methodologies for raising the nursery to coincide with the local cropping season and crop management practices were approximately uniform in all these trials[15,16].

At all locations, uniform crop growth was ensured by adjusting the time of planting and fertilizer application to suit the maturity period of test cultivars or the ecosystem where a particular experiment was conducted. However, locational influences on both crop growth and yield were expected. The assumption is that grain yield would be more uniform within defined maturity period and climatic regions. Therefore, the data sets were grouped into several classes: irrigated (early and medium maturity), rainfed lowlands (photoperiod sensitive or insensitive and late maturity), semideep–deep water (photoperiod sensitive and late maturity) and rainfed upland (early maturity). For experiments in India, data were recorded and maintained at DRR[15], and for the international experiments in other countries, data sets were obtained from the detailed reports of the International Rice Testing Programme[16]. For each year, the overall mean yield performances of selected genotypes across locations were computed. The conventional coefficient of variation (CV%) of each genotype as a stability measure[17,18] was also estimated. In international experiments, the stability performance of genotypes was computed by regression analysis[19]. Large rice areas in many countries were covered by the test locations and hence fixed effects in the linear model were assumed for genotypes and locations. Therefore, analyses were performed as per the fixed effect model. The genotypes were measured by the regression coefficient and differences in stability by deviations from the regression, and also supplemented by the CV.

Preliminary observations indicated a continual change in test cultivars in both national and international experiments, as rice improvement programmes actively encouraged introduction of many useful genes from germplasm into elite high-yielding cultivars. Locally well-adapted cultivars were used in all these experiments as checks. However, data sets from stress-free experiments were easily available for a few hundred cultivars evaluated for at least 3 years. The cultivars showing stability in yield over years, across environments and ecosystems were considered in terms of their photosensitivity or insensitivity and maturity, as well as the area under cultivation for characterizing them as universal genotypes for a specific mega-environment. For this study, the performance data on four cultivars (Rasi, Jaya, Swarnadhan and Sabita) at the national level and seven cultivars (Rasi, IR 36, IR 50, IR 8, Swarnadhan, Mahsuri and Savitri) globally, representing different maturity periods and ecosystems were chosen for illustrative purposes.

The performance of Rasi, an early maturing photoinsensitive cultivar (transplanted, 120 days), in wet (533 experiments) seasons in the All India coordinated experiments during 1970–94 was analysed (Table 1). Solar radiation and rainwater availability in the wet season could impose a stress on the crop. But, irrespective of locations, Rasi produced maximum grain yields of 10 t/ha (average across years, 3.9 t/ha).

Jaya, the first Indian high-yielding cultivar with maturity duration of 130 days, from seed to seed, was released for general cultivation in irrigated ecosystems in 1968. This photoinsensitive cultivar was routinely used as the standard check cultivar to evaluate elite breeding lines. Jaya was the best yielder in all these experiments[15]. The grain yield of Jaya in the wet seasons during 1970–94 was analysed. Jaya gave consistent and stable yields in 25 years of testing at many locations scattered all over the country. The linear regression performed with yield over time confirmed this stability ($r = 0.03^{ns}$). In these experiments, the coefficient of variation (CV%) across locations ranged from 19 to 47 (Table 1). The grain yield over locations varied from the lowest mean of 3.69 t/ha in 1984, to highest mean yield of 5.94 t/ha in 1994. Jaya produced a maximum grain yield of over 8 t/ha in 14 years, and nearly 7 t/ha in another 9 years. In 496 experiments, the overall mean grain yield over the years and locations was 4.5 t/ha. This indicated the ability of Jaya to overcome differences in environmental conditions.

The performance of Swarnadhan (photoinsensitive and late maturity, > 140 days) and Sabita (strongly photosensitive and late maturity, > 140 days) was also found to be stable in rainfed lowlands (Table 1). In 76 experiments, Swarnadhan produced mean grain yield ranging from 3.9 to 4.8 t/ha. The maximum grain yield obtained by Swarnadhan was nearly 10 t/ha. The overall mean grain yield across years and locations was 4.6 t/ha. In 49 experiments in semideep to deep-water rainfed lowland locations, Sabita produced mean grain yield ranging from 1.9 to 3.5 t/ha. The number of locations, however, was limited (4 to 12). Sabita recorded a maximum grain yield of 5 t/ha. The overall mean grain yield across years and locations was 2.8 t/ha.

**Table 1.** Performance of high-yielding rice cultivar bred for different mega-environments, in India during various years*

| | | Grain yield (t/ha) | | | |
|---|---|---|---|---|---|
| Year | No. of locations | Mean | Maximum | SEm | CV (%) |
| *Mega-environment-2* | | | | | |
| Rasi – an early maturing, photoinsensitive cultivar | | | | | |
| 1972 | 16 | 4.7 | 8.2 | 0.30 | 26 |
| 1973 | 8 | 4.7 | 6.3 | 0.42 | 25 |
| 1974 | 41 | 4.0 | 6.0 | 0.16 | 26 |
| 1975 | 36 | 3.5 | 6.0 | 0.18 | 32 |
| 1976 | 36 | 4.0 | 8.3 | 0.22 | 33 |
| 1977 | 36 | 3.9 | 6.2 | 0.18 | 27 |
| 1978 | 36 | 3.4 | 8.2 | 0.22 | 37 |
| 1979 | 54 | 3.9 | 6.5 | 0.15 | 29 |
| 1980 | 52 | 3.5 | 7.8 | 0.19 | 41 |
| 1981 | 47 | 3.5 | 6.8 | 0.20 | 41 |
| 1982 | 35 | 3.7 | 6.3 | 0.20 | 32 |
| 1983 | 65 | 3.4 | 10.0 | 0.20 | 47 |
| 1984 | 17 | 4.8 | 9.4 | 0.41 | 36 |
| 1985 | 38 | 3.4 | 6.8 | 0.23 | 41 |
| 1990 | 16 | 4.0 | 7.0 | 0.40 | 41 |
| Overall | 533 | 3.9 | 10.0 | – | – |
| *Mega-environment-3* | | | | | |
| Jaya – the first Indian high-yielding photoinsensitive medium maturing semidwarf cultivar | | | | | |
| 1970 | 24 | 4.90 | 8.61 | 0.29 | 29 |
| 1971 | 17 | 5.48 | 7.92 | 0.25 | 19 |
| 1972 | 14 | 5.68 | 8.76 | 0.31 | 20 |
| 1973 | 19 | 4.35 | 6.82 | 0.32 | 32 |
| 1974 | 26 | 3.88 | 5.76 | 0.24 | 32 |
| 1975 | 27 | 4.44 | 8.76 | 0.31 | 36 |
| 1976 | 23 | 4.30 | 7.43 | 0.28 | 31 |
| 1977 | 28 | 4.57 | 7.67 | 0.25 | 28 |
| 1978 | 33 | 4.47 | 8.03 | 0.26 | 34 |
| 1979 | 27 | 4.60 | 8.53 | 0.31 | 34 |
| 1980 | 29 | 4.02 | 7.35 | 0.31 | 41 |
| Jaya (*Continued*) | | | | | |
| 1981 | 29 | 4.25 | 8.94 | 0.26 | 33 |
| 1982 | 23 | 4.55 | 8.61 | 0.34 | 36 |
| 1983 | 23 | 4.63 | 8.25 | 0.30 | 31 |
| 1984 | 20 | 3.69 | 6.79 | 0.38 | 47 |
| 1985 | 20 | 4.31 | 8.28 | 0.44 | 45 |
| 1986 | 15 | 4.80 | 8.03 | 0.36 | 29 |
| 1987 | 16 | 4.58 | 8.07 | 0.44 | 38 |
| 1988 | 11 | 4.05 | 6.94 | 0.56 | 46 |
| 1989 | 14 | 4.11 | 8.24 | 0.46 | 42 |
| 1990 | 14 | 3.77 | 7.06 | 0.38 | 37 |
| 1991 | 13 | 4.85 | 6.89 | 0.34 | 25 |
| 1992 | 11 | 5.23 | 8.68 | 0.45 | 29 |
| 1993 | 8 | 4.51 | 5.86 | 0.33 | 21 |
| 1994 | 12 | 5.94 | 8.42 | 0.55 | 32 |
| Overall | 496 | 4.50 | 8.94 | – | – |
| *Mega-environment-4* | | | | | |
| Swarnadhan photoinsensitive and late maturing cultivar | | | | | |
| 1976 | 12 | 4.8 | 6.1 | 0.24 | 17 |
| 1977 | 16 | 4.8 | 9.9 | 0.49 | 41 |
| 1978 | 24 | 3.9 | 6.8 | 0.29 | 26 |
| 1979 | 24 | 4.7 | 6.4 | 0.22 | 23 |
| Overall | 76 | 4.6 | 9.9 | – | – |
| Sabita photosensitive and late maturing cultivar | | | | | |
| 1982 | 4 | 3.5 | 4.7 | 0.34 | 19 |
| 1983 | 8 | 3.0 | 4.6 | 0.32 | 30 |
| 1984 | 8 | 2.9 | 4.9 | 0.39 | 38 |
| 1985 | 8 | 3.0 | 4.9 | 0.28 | 27 |
| 1986 | 12 | 2.6 | 3.6 | 0.27 | 36 |
| 1987 | 9 | 1.9 | 2.9 | 0.17 | 27 |
| Overall | 49 | 2.8 | 4.9 | – | – |

Mega-environment-2 represents rainfed favourable uplands and irrigated areas requiring varieties with photoinsensitivity and nearly maturity (90–110 days).

Mega-environment-3 represents irrigated areas requiring varieties with photoinsensitivity and medium maturity (120–135 days).

Mega-environment-4 represents rainfed lowlands requiring varieties with photosensitivity or insensitivity and late maturity (> 140 days).

*Data derived from the all-India coordinated trials on varietal improvement[15].

A similar analysis was conducted using the data on some of the predominant cultivars with different maturity periods, in the international trials[16]. The stability parameters mean, *b* and $S^2_d$ were estimated. Data on seven cultivars, photoinsensitive and photosensitive, with varied maturity periods, are given in Table 2. These cultivars have been recommended for commercial cultivation: Rasi for rainfed uplands, and IR 36 and IR 50 for irrigated areas (photoinsensitive, early maturity, 110 days from seed to seed), IR 8 (photoinsensitive, medium maturity, 130 days) for irrigated ecosystem and Swarnadhan (photoinsensitive and late maturity, > 140 days), Mahsuri (essentially photoinsensitive and late maturity, > 140 days) and Savitri (weakly photosensitive and late maturity, > 140 days) for rainfed lowlands.

From 59 experiments in rainfed favourable uplands in 3–11 countries, the grain yield data on Rasi were evaluated. The experimental locations were spread from latitude 31°N to 6°S, longitude 122°E to 92°W, and altitude 7 to 1000 m above mean sea level (Table 2). The mean yields ranged from 1.9 to 3.6 t/ha. The maximum grain yield was 7.1 t/ha, recorded in 1978. In all the years of study, the regression coefficients were not statistically different from unity for Rasi.

The grain yield data sets for 16 years on the performance of IR 36 from 482 experiments in irrigated areas in

**Table 2.** Stability and wide adaptability of rice cultivars in different ecosystems across geographic boundaries in mega environments*

| Year | Country | No. of locations | Latitude (degrees) | Longitude (degrees) | Altitude (m above MSL) | Grain yield (t/ha) | | CV (%) | *b* | SE*b* | *R* | $S^2_d$ | Residual CV (%) |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | | | | Mean | Maximum | | | | | | |
| *Mega-environment-2* | | | | | | | | | | | | | |
| Cultivar: Rasi (photoinsensitive and early maturing) | | | | | | | | | | | | | |
| 1976 | 3 | 15 | 29N–12N | 121E–76E | 8–695 | 3.2 | 5.0 | 32.1 | 1.02 | 0.20 | 0.88 | 0.11 | 13 |
| 1977 | 11 | 20 | 31N–6S | 122E–5W | 7–626 | 3.0 | 6.2 | 63.8 | 0.93 | 0.56 | 0.41 | 0.61 | 29 |
| 1978 | 7 | 16 | 27N–3N | 122E–92W | 31–1000 | 3.6 | 7.1 | 61.4 | 1.02 | 0.08 | 0.96 | 0.18 | 15 |
| 1992 | 3 | 8 | 24N–7N | 90E–3E | 8–625 | 1.9 | 2.6 | 32.5 | 0.93 | 0.43 | 0.66 | 1.31 | 82 |
| Cultivar: IR 36 (photoinsensitive and early maturing) | | | | | | | | | | | | | |
| 1976 | 14 | 39 | 34N–6S | 121E–109W | 5–1000 | 4.6 | 8.8 | 30.5 | 0.86 | 0.10 | 0.81 | 0.62 | 19 |
| 1977 | 11 | 27 | 31N–14N | 121E–109W | 2–917 | 4.5 | 6.8 | 44.1 | 0.61 | 0.29 | 0.70 | 1.04 | 24 |
| 1978 | 17 | 26 | 31N–9S | 160E–100W | 2–185 | 4.8 | 8.2 | 29.3 | 0.98 | 0.08 | 0.93 | 0.20 | 10 |
| 1979 | 17 | 39 | 35N–9S | 160E–76W | 2–1000 | 4.5 | 8.0 | 30.1 | 0.88 | 0.09 | 0.86 | 0.44 | 16 |
| 1980 | 16 | 32 | 31N–9S | 160E–76W | 2–1167 | 4.8 | 8.0 | 35.9 | 0.86 | 0.14 | 0.74 | 0.94 | 22 |
| 1981 | 17 | 50 | 35N–6S | 128E–76W | 1–1000 | 4.6 | 8.7 | 29.6 | 0.94 | 0.07 | 0.89 | 0.36 | 14 |
| 1982 | 16 | 33 | 31N–26S | 121E–76W | 2–1150 | 4.6 | 7.7 | 35.3 | 1.18 | 0.11 | 0.89 | 0.29 | 13 |
| 1983 | 17 | 32 | 29N–6S | 128E–107W | 2–1000 | 4.7 | 7.8 | 26.8 | 0.80 | 0.08 | 0.88 | 0.56 | 16 |
| 1984 | 16 | 39 | 31N–3S | 128E–107W | 1–1500 | 4.9 | 8.7 | 32.0 | 0.95 | 0.07 | 0.92 | 0.35 | 13 |
| 1986 | 12 | 29 | 30N–21S | 119E–3E | 2–1500 | 4.8 | 8.9 | 32.6 | 0.94 | 0.07 | 0.93 | 0.33 | 12 |
| 1987 | 14 | 23 | 32N–8S | 120E–15W | 3–1200 | 4.0 | 7.3 | 34.8 | 1.08 | 0.07 | 0.95 | 0.20 | 11 |
| 1988 | 14 | 24 | 37N–5N | 121E–3E | 1–497 | 4.4 | 7.0 | 29.2 | 1.00 | 0.09 | 0.92 | 0.27 | 12 |
| 1989 | 9 | 20 | 33N–5N | 121E–3E | 2–716 | 4.5 | 9.9 | 51.2 | 1.40 | 0.06 | 0.98 | 0.22 | 11 |
| 1990 | 13 | 36 | 32N–6S | 121E–3E | 1–387 | 4.5 | 8.9 | 41.1 | 1.18 | 0.07 | 0.96 | 0.11 | 7 |
| 1991 | 7 | 11 | 24N–6S | 121E–3E | 5–427 | 4.5 | 7.2 | 32.4 | 0.99 | 0.08 | 0.97 | 0.13 | 8 |
| 1992 | 11 | 22 | 24N–5N | 121E–28E | 2–608 | 4.6 | 8.3 | 36.5 | 1.03 | 0.05 | 0.98 | 0.09 | 7 |
| Cultivar: IR 50 (photoinsensitive and early maturing) | | | | | | | | | | | | | |
| 1980 | 16 | 32 | 31N–9S | 160E–76W | 2–1167 | 4.7 | 9.4 | 33.6 | 0.87 | 0.12 | 0.79 | 0.78 | 20 |
| 1981 | 15 | 33 | 32N–30S | 121E–76W | 2–1200 | 4.4 | 7.9 | 39.9 | 1.11 | 0.08 | 0.93 | 0.28 | 14 |
| 1982 | 18 | 34 | 31N–25S | 128E–3E | 2–1150 | 4.8 | 9.0 | 37.4 | 1.13 | 0.10 | 0.89 | 0.64 | 20 |
| 1983 | 18 | 44 | 38N–16S | 120E–107W | 1–1000 | 4.8 | 10.4 | 37.2 | 1.04 | 0.09 | 0.87 | 0.53 | 17 |
| 1984 | 17 | 41 | 36N–3S | 121E–76W | 1–1200 | 4.6 | 9.2 | 45.9 | 1.08 | 0.06 | 0.95 | 0.33 | 14 |
| 1985 | 16 | 34 | 38N–25S | 128E–107W | 1–2000 | 5.0 | 9.2 | 35.3 | 1.21 | 0.01 | 0.95 | 0.31 | 11 |
| 1986 | 10 | 25 | 35N–11N | 128E–8E | 2–1500 | 5.3 | 10.8 | 32.0 | 1.05 | 0.08 | 0.94 | 0.35 | 11 |
| 1987 | 14 | 24 | 36N–7N | 128E–15W | 2–427 | 5.0 | 8.3 | 32.7 | 1.05 | 0.07 | 0.96 | 0.22 | 9 |
| 1988 | 15 | 27 | 36N–7N | 128E–3E | 1–1650 | 4.5 | 8.2 | 30.7 | 1.17 | 0.12 | 0.89 | 0.45 | 15 |
| 1989 | 11 | 26 | 35N–7N | 128E–3E | 1–1250 | 4.2 | 9.2 | 40.1 | 0.91 | 0.07 | 0.94 | 0.35 | 14 |
| 1990 | 15 | 25 | 37N–6S | 128E–3E | 0–950 | 4.8 | 9.0 | 34.2 | 0.95 | 0.08 | 0.93 | 0.36 | 14 |
| 1991 | 11 | 26 | 7N–25S | 121E–3E | 0–2000 | 4.5 | 9.7 | 37.7 | 1.09 | 0.07 | 0.95 | 0.23 | 11 |
| 1992 | 4 | 22 | 24N–5N | 121E–28E | 2–608 | 4.6 | 8.9 | 35.6 | 0.96 | 0.08 | 0.94 | 0.28 | 12 |
| *Mega-environment-3* | | | | | | | | | | | | | |
| Cultivar: IR 8 (photoinsensitive and medium maturing) | | | | | | | | | | | | | |
| 1977 | 11 | 28 | 31N–3N | 121E–107W | 2–1000 | 4.4 | 7.5 | 49.4 | 0.95 | 0.25 | 0.62 | 1.21 | 24 |
| 1978 | 11 | 26 | 27N–6S | 121E–109W | 2–263 | 4.3 | 8.7 | 46.3 | 1.15 | 0.08 | 0.95 | 0.28 | 12 |
| 1979 | 9 | 37 | 33N–6S | 106E–76W | 5–1000 | 4.2 | 6.9 | 38.9 | 1.05 | 0.08 | 0.90 | 0.35 | 14 |
| 1980 | 9 | 25 | 26N–6S | 120E–76W | 5–1167 | 4.1 | 7.7 | 41.3 | 1.13 | 0.10 | 0.92 | 0.25 | 11 |
| *Mega-environment-4* | | | | | | | | | | | | | |
| Cultivar: Swarnadhan (photoinsensitive and late maturing) | | | | | | | | | | | | | |
| 1977 | 6 | 10 | 27N–14N | 100E–109W | 2–58 | 4.9 | 7.5 | 42.2 | 1.27 | 0.26 | 0.86 | 1.25 | 23 |
| 1978 | 6 | 7 | 27N–3N | 105E–76W | 2–1000 | 5.4 | 8.9 | 44.0 | 1.04 | 0.09 | 0.98 | 0.23 | 9 |
| 1979 | 5 | 14 | 24N–3N | 102E–76W | 2–1000 | 4.6 | 7.5 | 39.4 | 1.17 | 0.07 | 0.98 | 0.14 | 8 |
| 1980 | 7 | 12 | 27N–3N | 106E–76W | 2–1000 | 4.3 | 7.1 | 46.9 | 1.18 | 0.11 | 0.96 | 0.35 | 14 |
| 1982 | 7 | 8 | 27N–6N | 102E–6E | 5–1150 | 3.3 | 6.8 | 43.6 | 0.81 | 0.43 | 0.55 | 5.07 | 68 |
| 1983 | 5 | 14 | 27N–7N | 123E–80E | 5–263 | 3.3 | 5.9 | 39.2 | 1.20 | 0.13 | 0.93 | 0.65 | 25 |

*(continued)*

**Table 2.** (*Continued*)

| | | | | | | | | | | | | | |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| Cultivar: Mahsuri (essentially photoinsensitive and late maturing) | | | | | | | | | | | | | |
| 1979 | 5 | 14 | 24N–3N | 100E–76W | 2–1000 | 4.4 | 6.9 | 36.1 | 0.98 | 0.10 | 0.94 | 0.32 | 13 |
| 1980 | 7 | 12 | 27N–3N | 106E–76W | 2–1000 | 4.2 | 7.6 | 42.4 | 1.01 | 0.11 | 0.95 | 0.26 | 13 |
| 1981 | 5 | 10 | 26N–10N | 123E–87E | 8–152 | 3.2 | 5.8 | 38.1 | 1.01 | 0.13 | 0.94 | 0.18 | 13 |
| 1982 | 7 | 8 | 27N–6N | 120E–6E | 5–1150 | 3.4 | 5.0 | 34.0 | 0.69 | 0.42 | 0.55 | 0.90 | 27 |
| 1983 | 5 | 14 | 27N–7N | 123E–80E | 5–263 | 3.1 | 4.5 | 33.7 | 0.78 | 0.18 | 0.78 | 0.44 | 22 |
| 1984 | 5 | 13 | 27N–10N | 104E–85E | 8–408 | 3.3 | 4.8 | 25.0 | 0.82 | 0.17 | 0.82 | 0.27 | 16 |
| 1985 | 5 | 13 | 26N–11N | 103E–79E | 8–215 | 3.3 | 5.1 | 35.0 | 0.87 | 0.08 | 0.95 | 0.11 | 10 |
| 1986 | 4 | 7 | 27N–6N | 103E–84E | 5–200 | 3.4 | 4.5 | 24.0 | 0.88 | 0.16 | 0.88 | 0.67 | 24 |
| 1987 | 6 | 11 | 27N–14N | 121E–84E | 13–144 | 2.8 | 4.1 | 29.2 | 0.75 | 0.20 | 0.78 | 0.28 | 19 |
| 1988 | 6 | 10 | 27N–12N | 121E–84E | 8–857 | 2.9 | 4.2 | 32.4 | 1.02 | 0.14 | 0.93 | 0.04 | 7 |
| 1989 | 5 | 11 | 25N–8N | 121E–13W | 22–170 | 2.7 | 5.3 | 64.2 | 1.09 | 0.10 | 0.97 | 0.19 | 16 |
| 1990 | 5 | 10 | 27N–8N | 121E–84E | 3–200 | 2.8 | 4.3 | 45.8 | 0.88 | 0.12 | 0.93 | 0.31 | 19 |
| 1992 | 5 | 7 | 25N–7N | 121E–3E | 21–290 | 2.6 | 4.0 | 37.9 | 0.94 | 0.26 | 0.85 | 0.27 | 20 |
| 1993 | 5 | 6 | 23N–7N | 121E–3E | 8–200 | 3.2 | 4.7 | 32.7 | 0.78 | 0.16 | 0.93 | 1.97 | 50 |
| Cultivar: Savitri (weakly photosensitive and late maturing) | | | | | | | | | | | | | |
| 1977 | 6 | 10 | 27N–14N | 100E–109W | 2–58 | 4.5 | 8.4 | 54.5 | 1.60 | 0.25 | 0.91 | 0.39 | 15 |
| 1978 | 6 | 7 | 27N–3N | 100E–76W | 2–1000 | 5.0 | 10.3 | 63.2 | 1.54 | 0.06 | 1.00 | 0.10 | 7 |
| 1979 | 5 | 14 | 24N–3N | 100E–76W | 2–1000 | 5.0 | 7.1 | 32.0 | 1.04 | 0.06 | 0.98 | 0.19 | 10 |
| 1980 | 7 | 12 | 27N–3N | 106E–76W | 2–1000 | 4.2 | 7.7 | 43.1 | 1.06 | 0.10 | 0.96 | 0.21 | 12 |

Mega-environment-2 represents rainfed favourable uplands and irrigated areas requiring varieties with photoinsensitivity and early maturity (90–110 days).

Mega-environment-3 represents irrigated areas requiring varieties with photoinsensitivity and medium maturity (120–135 days).

Mega-environment-4 represents rainfed lowlands requiring varieties with photosensitivity or insensitivity and late maturity (> 140 days).

*Data derived from the International Rice Testing Programme/International Network on Genetic Evaluation of Rice[16].

7–17 countries were analysed. The experimental locations were spread from latitude 37°N to 26°S, longitude 160°E to 109°W, and altitude 1 to 1500 m above mean sea level. The mean grain yield of IR 36 ranged from 4.0 to 4.9 t/ha. The maximum yield was 9.9 t/ha, recorded in 1989. The data sets on IR 50 from 393 experiments in irrigated areas during 1980–1992 in 4–18 countries were analysed. The experimental locations were spread from latitude 38°N to 30°S, longitude 160°E to 107°W and altitude 0 to 2000 m above mean sea level. The mean yield ranged from 4.2 to 5.3 t/ha. The maximum grain yield was 10.8 t/ha, recorded in 1986. The regression coefficients for IR 36 and IR 50 were not statistically different from unity in all the years of study, except for IR 36 in 1989 and IR 50 in 1985.

In the irrigated medium maturity group, IR 8 was chosen for the study. The yield data from 116 experiments conducted in 9–11 countries were used for evaluating the performance of this cultivar (Table 2). The experimental locations were spread from latitude 33°N to 6°S, longitude 121°E to 109°W and altitude 2 to 1167 m above mean sea level. The maximum grain yield was 8.7 t/ha, recorded in 1978. The mean grain yield ranged from 4.1 to 4.4 t/ha. The regression coefficients for IR 8 were not statistically different from unity in all the years of study.

In rainfed lowlands, late maturity group cultivars differentially sensitive to photoperiod such as Swarnadhan (insensitive), Mahsuri (essentially insensitive) and Savitri (weakly sensitive) were considered for analysis. The data sets from 65 experiments during 1977–83 with Swarnadhan were available. The experimental locations were spread from latitude 27°N to 14°N, longitude 123°E to 109°W and altitude 2 to 1150 m above mean sea level. The mean grain yield ranged from 3.3 to 5.4 t/ha, with a maximum grain yield of 8.9 t/ha recorded in 1978 (Table 2). The data on Mahsuri evaluated in 146 experiments in 4–7 countries and at a maximum of 14 locations were analysed. The experimental locations were spread from latitude 27°N to 3°N, longitude 123°E to 76°W and altitude 2 to 1000 m above mean sea level. The mean grain yield ranged from 2.6 to 4.4 t/ha. The maximum grain yield was 7.6 t/ha recorded in 1980.

Savitri was evaluated in 43 experiments in 5–7 countries. The experimental locations were spread from latitude 27°N to 3°N, longitude 106°E to 109°W and altitude 2 to 1000 m above mean sea level. The mean yield ranged from 4.2 to 5.0 t/ha. The maximum grain yield was 10.3 t/ha, recorded in 1978. The regression coefficients for Swarnadhan, Mahsuri and Savitri were not statistically different from unity in all the years of study, except for Savitri in 1977 and 1978.

Most applied plant-breeding programmes evaluate many genotypes in different environments (years and locations) to identify desirable genotypes for release. A constant annual yield of a crop grown by farmers is one of the most important issues facing world agriculture and food supply. Stability is equally important as yield itself. Several rice genotypes bred at both national and international centres (Tables 1 and 2) were determined as stable. This indicates that breeding for high-yielding stable lines with different maturity periods is feasible. The regression coefficients of nearly unity in all cultivars investigated here indicated the stability of these cultivars across the test locations in different countries. The estimated values for standard error indicated that *b* values did not deviate significantly from unity in these cultivars. The wide range of latitude and altitude under which these cultivars were found to perform consistently shows their ability to cross geographical boundaries. The varied soil types, meteorological conditions and cultural practices determine yields at each location, but the performance of the test cultivars does not change. In the all-India coordinated experiments and in the international cultivar trials, the sets of cultivars in different groups normally vary. Despite this handicap and the need to compete with newer elite cultivars each year, the *b* values near 1 in different groups over years further confirm the stability of these high-yielding cultivars and their ability to adapt to varied environments.

All the considered genotypes have been released for commercial cultivation in several countries[13,20]. And due to their yield stability, these genotypes now occupy sizable areas. Jaya was released in Vietnam and in sub-Saharan African countries, Ivory Coast, Mali and Senegal. Rasi spread to Nepal as *Bindeswari* and as *IET 1444* to Tanzania and Nigeria. By 1982, IR 36 with genetic resistance to 15 pests and environmental stresses was grown under a dozen names in 13 million hectares of rice land[20]. IR 36 occupied 5 m ha in Indonesia, 2.3 m ha in Philippines, 2.1 m ha in Vietnam, 0.7 m ha in Cambodia and > 2 m ha in other countries in Asia. IR 8 has been released for commercial cultivation in several countries: Myanmar (*Yagyaw 1*), India, Indonesia (*PB 8*), Iraq (*Zarate 8*), Nepal, Philippines and Vietnam (*Nong Nghiep 8*). IR 8 was also introduced and grown in Costa Rica (1972, entire rice area), Cuba (1971, 91% of rice area), Honduras (1973, 2500 ha), and Laos (1966, 1200 ha). IR 8 was also grown in Milagro Filipino (Mexico), Chato in Ecuador, Colombia (1968) and Dominican Republic (1966). Mahsuri was derived from hybridization efforts of the *indica–japonica* project in Malaysia, where it occupied 15% of the rice area by 1982. It spread to rainfed lowlands under the names *Mahsuri* and *Ponni* in India, *Pajam* in Bangladesh, *Manawhari* in Myanmar and *Masuli* in Nepal[21,22]. Brundi has released Savitri for the Sub-Saharan Africa[13].

Yields for a range of locations varying in latitude from 31 to 6°N were reduced by 10–20%, with a rise in temperature of 1–2°C, during the November–December harvest period[23]. Also, yield estimates were most severely affected at higher latitudes. In this study also, particularly at low latitude or at high altitude, as ambient temperature fell, the mean yield increased in most cases. However, occasional exceptions at contrasting latitude and altitude positions were found, where the mean grain yields remained static in international experiments. For example, during 1981, at Taichung, Taiwan (24°N and 83 m above mean sea level) and Palmira, Colombia (3°N, 1000 m above mean sea level), IR 50 produced similar grain yields. Also, the differences in latitude at Rangsit, Thailand (14°N) and Salamagna, Mozambique (26°S), and elevation at Kapurthala, India (228 m above mean sea level) and Palmira, Colombia (1000 m above mean sea level) did not influence the grain yield of IR 36 during 1982 (ref. 16). Ecogeographic grouping of locations during wet season does not appear to provide any advantage[24]. It has been clearly established in rice[24,25] and sorghum[26] that cultivar adaptability and stability are highly correlated.

The selection for low genotype × environment interactions and high yield resulted in the development of genotypes that, although classified as widely adapted, are considered to be truly adapted to environments where their high yield potential can be expressed. A wheat cultivar Bezostaya 1, was reportedly grown in about 6 m ha in USSR in the 1970s[27]. Several semi-dwarf wheat cultivars selected from Centro Internacional de Mejoramiento de Maiz y Trigo, Mexico, DF (CIMMYT) cross 8156 were also known to have spread over 5 m ha (ref. 20). The spread of such wheat genotypes over a wide geographical area has been often taken as a demonstration of wide adaptation, without taking into account that a large fraction of this area is very similar or made similar by the use of irrigation and/or fertilizer. To a large extent, the term ‘wide adaptation’ has been used in a geographical rather than in an environmental sense[28]. A mega-environment includes environments with a common denominator that makes them distinct from others, such as rainfed lowland rice vs irrigated rice environments. Defined in this way, mega-environments can really embrace large geographical areas. The differences in response to photoperiods, ambient temperatures and maturity duration decide the adaptive traits of cultivars in a macro- or mega-environment[29,30]. In breeding for spring wheat, CIMMYT adopted the concept of six mega-environments, defined as broad areas characterized by similar biotic and abiotic stresses, cropping system requirements and consumer preferences[31].

The ability of a rice cultivar to spread over a highly specific ecological niche into mega-environments can be illustrated with the universal genotypes identified in this study. The results clearly showed that all these genotypes were able to cross geographic boundaries and spread over latitudes and still record stable and high yields. The mega-environments where these genotypes spread are governed by the photoinsensitivity or photosensitivity and maturity duration. A photoinsensitive cultivar like Rasi, for example, gave stable and high yields at different locations over the years (Table 1). This cultivar was bred for irrigated areas requiring early maturity. Rasi registered a stable yielding ability in rainfed favourable upland also (Table 2). The regression coefficient *b* was not statistically different from unity, in the analysis of the grain yield data sets from the international experiments. Further in 1991, Rasi demonstrated its ability to produce stable and high yields in rainfed shallow lowlands[16]. In Ethiopia, Rasi was found to produce higher yields in midhills under both irrigated and rainfed areas, with an elevation ranging from 800 to 2000 m above mean sea level[32]. In West Africa, Rasi recorded stable and high yields in rainfed favourable uplands, in direct-seeded irrigated ecosystem and in transplanted ecosystem, in both plains and hills[33]. For the rainfed unfavourable upland, which is known to be fragile and unfit for rice cultivation[34], our study could not identify any universal genotype. Three decades ago Barker *et al.*[35] had concluded that it is scientifically more difficult and uneconomical to develop new varieties for unfavourable production environments.

The present study showed that late maturing group cultivars differentially sensitive to photoperiod such as Swarnadhan, Mahsuri and Savitri, also produced stable and high yields in many experiments, in rainfed lowlands. These genotypes have been evaluated for a number of years at multiple locations, in different rice-growing countries around the world. At these experimental locations, variations are to be expected in the depth of standing water and duration of flooding. Further variations are also expected in the time of occurrence of early drought or actual submergence or flooding. However, this study demonstrated the yield stability of all these genotypes. In 1982 and 1983, Sabita was evaluated in 10 international experiments in shallow rainfed lowlands also. This photosensitive late maturing cultivar ranked first with a mean grain yield of 3.1 t/ha, among from 11 test entries[16]. Sabita recorded such stable yielding ability in eight other experiments during 1982 and 1983 in waterlogged areas also[15] and gave the highest grain yields in the second international deep-water experiments in 1984.

Mega-environments are not limited, therefore, either by the ecosystem or by geographical continuity or discontinuity. In fact, universal genotypes with wide adaptability and stable yielding ability were available, but not recognized for a long time. One of the grandparents used for deriving Mahsuri was Shinriki. This leading *rono* cultivar, a high fertilizer-responsive and short-stature cultivar, was selected in Japan in 1877. Shinriki was introduced in US in 1902 and was extensively grown in Louisiana and Texas until 1910 (ref. 36). Shinriki was apparently a widely adapted cultivar, with an ability to yield high in a mega-environment. Its derivative Mahsuri, essentially photoinsensitive and with late maturity, however, dominated the rainfed lowlands around the globe, although released for commercial cultivation in 1965, in Malaysia for the double-cropped irrigated areas.

The mangrove swamps (> 1.0 m ha) in the West African countries of Gambia, Guinea, Guinea-Bissau, Nigeria, Senegal and Sierra Leone that lie between latitude 20°N and 5°N, adjacent to rivers and creeks along the Atlantic coast can be cited as another example of a mega-environment. A wide range of climatic conditions occurs in this mangrove swamp area, from dry tropical climate with about 800 mm rainfall (southern Senegal) to a humid climate with nearly 4000 mm rainfall in Nigeria. ROK 5, a high-yielding cultivar bred at Rokupr[37] was cultivated in large areas for more than a decade in Sierra Leone, Guinea, Guinea-Bissau, Gambia and Senegal. The ability of ROK 5 to mature prior to intrusion of salt water and avoid salt damage enabled it to spread across the Atlantic coast[38], as a universal genotype for this mega-environment.

The environmental diversity within the deep-water areas has produced a multitude of different cultivars, some of which are apparently planted over fairly large areas. RD 19 (BKN 6986–147–2) derived from a cross IR 262/Pin Gaew 56 was released in Thailand in 1980, for traditional deep-water and floating areas. It is strongly photoperiod-sensitive with good tillering, rooting and kneeing ability. RD 19 is also fairly drought-tolerant and produces a small canopy above the water. This plant type replaced many existing traditional cultivars in mega-environment with flooding from 50 to 120 cm in South and South-east Asia[39], requiring a cultivar with photosensitivity and late maturity period. A sister selection of RD 19 was also released as *Yenet-6* in Myanmar, for cultivation under such a mega-environment.

Many cultivars like TN 1 and IR 20, spread and occupied vast areas and produced stable yields in various environments[22]. Blue Belle and Blue Bonnet, that originated in USA, are also commercially produced in large areas in differing environments in Latin America[40] and Africa[33]. BG 367–4 was a stable and high-yielding cultivar developed in Sri Lanka. It recorded stable yields in rainfed, direct-seeded upland and in transplanted areas in the plains under the irrigated ecosystems or in the hills[16,41]. These cultivars also represent the universal genotypes for specific mega-environments.

As farmers adopt modern cultivars and improved cultural practices, they generally shift to monoculture and this has been assumed to lead to genetic simplification of rice cultivated in many farmlands. When a single cultivar is planted over large areas, vulnerability to pests and diseases has been speculated[27]. A large number of improved rice cultivars released since the early

1940s trace maternally to *Cina*[42]. Other popular land races used in crosses include Latisail and Peta. Chang and Vergara[43] also expressed concern about the lack of diversity of cytoplasm. However, the genetic makeup of the universal genotypes discussed in this study includes female progenitors, with *Cina* (IR 36, IR 50, IR 8, Swarnadhan, and Savitri); and *Mayang Ebos* cytoplasm (Mahsuri). Including Jaya, Rasi, IR 8, IR 36, IR 50 and Savitri, most semidwarf improved rice cultivars developed worldwide, derive their dwarfing gene from the Chinese dwarf *DGWG*. However, after 50 years of continued use, no weakness in *Cina* cytoplasm has been detected so far[42,44].

The genetic makeup of these stable universal genotypes shows considerable variation. Mahsuri is a derivative of a cross between *indica* – Mayang Ebos and *japonica* – Taichung 65 (Kameji × Shinriki). Neither *Cina* cytoplasm nor *DGWG* genes are present in Mahsuri. Cultivars genetically equipped with high yield potential will have an ability to tolerate to an extent, the general field pressures. Thus, the apparent susceptible symptoms may not make a visible dent in the field. In truth, no major rice crop failure has occurred recently on the scale of the Great Bengal famine or the Irish potato famine. The production-oriented surveys covering a rice area of 42 m ha in India[44] and the international rice crop monitoring tour reports[45], have reported no rice crop failure in large areas. These reports also list many different rice cultivars under cultivation at any one location. The widely held hypothesis that the green revolution led to biological simplification has not been confirmed so far[46]. Although *Cina* cytoplasm or *DGWG* genes may be present in many cultivars, intensive efforts in building up gene pools in modern rice cultivars through the use of germplasm collections must have insulated them and provided them with resilience and variations. The remarkable diversity attained in rice-breeding lines at several centers, was illustrated with the quick success in releasing cultivars resistant to newly discovered gall midge biotype within a year[47]. Globally coordinated rice improvement programmes that facilitate a regular exchange of gene sources, have contributed to an increase in the biodiversity[48]. This diversity in cultivars has successfully prevented the vulnerability and yield instability of rice in mega-environments.

With the arrival of high-yielding semidwarf rice in 1966, extensive studies on rice lands led to the creation of many ecosystems and a multitude of breeding objectives associated with pushing yields and total production. However, the breeding programmes have had little success in spite of many studies on the genetic architecture of the seed yield, estimation of the gene action traits developmentally associated with seed yield or the various selection indices formulated. The present study using data sets from 2646 experiments established 10 t/ha as the maximum realizable grain yield. The photoinsensitive universal genotypes, IR 8 (refs 49, 50) and Jaya[47] with medium maturity period and maximum yield not exceeding the 10 t/ha limit, were actually developed in 1966 and 1968, respectively. None of the genotypes developed for the various assumed ecosystems surpassed this limit. The reason for this dismal performance after spending research resources all over the world at so many breeding sites could be the plethora of breeding objectives and target ecosystems. The idea of location-specific research has been extended too far[51]. A generalized approach is most often discouraged. In the evaluation of breeding stock, all checks used have good general adaptability[18]. If wide adaptability and yield stability had been the main objectives and maximum priority given to developing high-yielding universal genotypes for mega-environments, quite possibly the next phase of yield levels might have been easily attained. Gauch and Zobel[52] concluded by analysing Louisiana corn trial data, that a small and workable number of mega-environments are enough to exploit interaction and increase yields. We therefore, suggest that the area under rice can be regrouped into four mega-environments as: mega-environment-1, representing rainfed unfavourable uplands requiring varieties with photoinsensitivity and very early maturity (< 90 days); mega-environment-2, representing rainfed favourable uplands and irrigated areas requiring varieties with photoinsensitivity and early maturity (90–110 days); mega-environment-3, representing irrigated areas requiring varieties with photoinsensitivity and medium maturity (120–135 days); and mega-environment-4, representing rainfed lowlands requiring varieties with photosensitivity or insensitivity and late maturity (> 140 days). This delineation can motivate rice breeders to push yields of universal genotypes beyond the 10 t/ha barrier.

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