Seed Production Environment, Time of Harvest, and the Potential Longevity of Seeds of Three Cultivars of Rice (*Oryza sativa* L.)

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Changes in seed quality (assessed by potential longevity, i.e. the value of the seed lot constant K_i of the seed viability equation) in three contrasting cultivars of rice (*Oryza sativa* L.) were monitored during seed development and maturation in two temperature regimes, *viz* 28/20 °C and 32/24 °C (12/12 h), provided by controlled environments. Mass maturity (defined as the end of the seed-filling phase) varied only between 18 and 20 d after 50 % anthesis. In five of the six treatment combinations maximum potential longevity was not achieved until 12–19 d after mass maturity. In contrast, the maximum potential longevity of seeds of a *japonica* rice cultivar produced in the warmer regime was obtained in the first harvest after mass maturity. After mass maturity, the potential longevity of the *japonica* rice seed lots produced in the warmer environment was much less than that for the cooler environments. Maximum potential longevity was also consistently greater in the cooler than the warmer regime for the two *indica* cultivars, although the difference in K_i was small (0·3–0·5). The deleterious effect of increase in temperature on seed quality development was not detected until after mass maturity. Maximum potential longevity in the cooler regime was greatest in the glutinous *indica* cultivar ($K_i = 3·9$) and least in the *japonica* cultivar ($K_i = 3·1$). It is concluded that the *japonica* cultivar is not as well adapted to warm seed production regimes as the *indica* cultivars. Consequently, subject to confirmation, this research suggests that the seed production of *japonica* cultivars for long-term genetic conservation should be undertaken, whenever possible, in warm temperate environments.

Key words: *Oryza sativa* L., rice, genebanks, seed development, seed storage, seed longevity, temperature.

INTRODUCTION

There is now considerable evidence in several cereals (Kameswara Rao *et al.*, 1991; Pieta Filho and Ellis, 1991*a*; Ellis and Pieta Filho, 1992) and also other crops (Demir and Ellis, 1992*a, b*, 1993; Zanakis, Ellis and Summerfield, 1994) that developing and maturing seeds do not attain maximum ability to survive air-dry storage until some time after mass maturity—defined as the end of the seed-filling phase (Ellis and Pieta Filho, 1992). Several other facets of seed quality have also been shown to continue to improve during the natural seed maturation that occurs subsequent to mass maturity; for example, field emergence ability in barley (*Hordeum vulgare* L.) (Pieta Filho and Ellis, 1991*b*), and seedling growth potential in pepper (*Capsicum annuum* L.) (Demir and Ellis, 1992*b*). These results contradict the general hypothesis of Harrington (1972) that seed quality reaches maximum values at the end of the seed-filling phase and that thereafter viability and vigour decline—even though at least the first part of this hypothesis is supported by some recent investigations (for example, TeKrony, Egli and Phillips, 1980; Rasyad, Van Sanford and TeKrony, 1990).

In recent investigations on the lower limit to the negative logarithmic relation between seed longevity and moisture content in air-dry storage in three ecogeographic races of rice (*Oryza sativa* L.) it was found that *japonica* cultivars had poorer longevity characteristics than those of either *indica* or *javanica* cultivars (Ellis, Hong and Roberts, 1992)—as Chang (1991) had suggested earlier. In that work, seed storage longevity was assessed in two ways. First by potential longevity as defined by the value of the seed lot constant K_i in the following equation which describes the seed survival curve in any one (constant) air-dry environment:

$$v = K_i - p/\sigma \qquad (1)$$

where v is probit percentage viability after p days in storage and σ is the standard deviation of the frequency distribution of seed deaths in time (d). Second, by comparing the negative logarithmic relations between seed longevity (σ) and moisture content (m, % wet basis) at one temperature:

$$\log_{10} \sigma = K - C_w \log_{10} m \qquad (2)$$

where K is an intercept constant and C_w is the sensitivity of longevity to moisture content (Ellis and Roberts, 1980*a*). Both K_i and K were poorer for *japonica* compared with *indica* cultivars (Ellis *et al.*, 1992). Those investigations used seed lots produced at the International Rice Research Institute (IRRI) at Los Baños, Philippines (14° N).

Whereas the *indica* and *javanica* rices evolved in climates roughly similar to those pertaining at Los Baños, the *japonica* rices evolved in somewhat cooler, more temperate environments (Purseglove, 1972; Yoshida, 1983; Chang, 1989). This led us to question whether the seed storage characteristics of *japonica* rices were intrinsically poorer than *indica* rices or whether the results described above were

TABLE 1. *Information on the cultivars of rice grown, and initial seed stocks*

IRGC* accession number	Cultivar name	Varietal type	Comments	Country of origin	Mean seed dry weed (mg)	Normal germination† (%)
17826	Ketan Amnera	*indica*	glutinous	Indonesia	28·4	100
42576	Taipei 309	*japonica*	non-glutinous	China-Taiwan	21·3	78
44474	Intan	*indica*	non-glutinous	Indonesia	25·6	99

* International Rice Germplasm Center (IRRI, Philippines).
† Tested at 34/11 °C (16/8 h) for 28 d.

a consequence of the seed production environment. Accordingly, the hypothesis that potential seed longevity is maximal at mass maturity and subsequently declines was tested in *japonica* and *indica* cultivars in two temperature regimes: one mimicking Los Baños (the site of the world's major rice genebank) and a cooler regime mimicking Tsukuba (36° N) in Japan (the site of the Genebank, National Institute of Agrobiological Resources). Two *indica* cultivars were selected for study in order to determine the potential effect of the glutinous character on seed quality development and potential longevity.

MATERIALS AND METHODS

Seeds of three cultivars of rice (Table 1) were provided by IRRI. Plants were grown in pots in two plastic tunnel houses at Reading, UK, with temperatures controlled at 28/20 °C (12/12 h) in one tunnel house and 32/24 °C 12/12 h) in the second. Temperatures were logged continuously at several points in both tunnels and were maintained to within 0·5 °C of the nominal temperatures (except briefly during the pre-flowering period, when temperatures were occasionally as much as 4 °C warmer than nominal values in the cooler regime during a 3 d period, between 33 and 36 d after sowing, when ambient temperatures were particularly warm—because cooling was by ventilation with ambient air). Within each tunnel, the three cultivars were grown as separate 'crops'.

Plant husbandry and culture

All seed stocks were graded by eye and the smallest seeds within each accession discarded. About 800 seeds of each accession were soaked in 100 ml deionized water for 8 h at 20 °C, and then incubated moist at 25 °C for 40 h. The objective of this treatment was to provide seed germinating synchronously—such that visible germination was just apparent. For each cultivar, five germinating (roots and shoots just visible) seeds were sown into each of 108 18 cm diameter (2·0 l) plastic pots. The growth medium and its preparation was that described by Summerfield *et al.* (1992). One seed was sown in the centre of each pot, and the remaining four on the corners of a 3 cm square. The seeds were covered with 0·2 l of crushed (0·6 cm) gravel. The pots were arranged in 18 rows of six pots each on 25 cm (centre to centre) spacings. The pots on the outside of the rows were wrapped in aluminium foil (to prevent heating by solar gain). Seeds were sown on 10 Apr. in the cooler regime and on 22 Apr. 1992 in the warmer regime. At 13 d after sowing

(when seedlings were 10–15 cm tall) the pots were flooded and subsequently irrigated automatically (six times per day initially, then 10 times per day from 60 d after sowing) with a nutrient solution, such that irrigation caused the flooded pots to overflow, using the system devised by Summerfield *et al.* (1992); the pH was controlled at < 6·5. The number of seedlings was reduced to three per pot at 16 d after sowing. Hence the plant population density was 48 plants m^{-2} thereafter.

From 13 d after sowing in the warmer regime and from 25 d after sowing in the cooler regime, a photoperiod of 12 h d^{-1} was imposed with a blackout; additional forced ventilation was provided beneath this blackout in order to maintain temperature control. Photoperiod and day/night temperature control were synchronised. Photoperiod control was maintained until all plants had flowered; the durations of the initial period in natural daylengths (i.e., without photoperiod control) was based on estimates of the photoperiod-insensitive pre-inductive phase of rice plant development for contrasting genotypes provided by Collinson *et al.* (1992).

The plants were staked with canes in order to prevent lodging. Plants were inspected daily; at four-weekly intervals (or more frequently when necessary) the tunnel houses were fumigated with an acaricide in order to control red spider (the only significant problem encountered whilst growing the plants). The progress of flowering and the date of 50% anthesis were recorded. Flowers that appeared uncharacteristically early or late (mainly on plants on the outside of rows) were tagged; seeds from these panicles were excluded from subsequent investigation.

Seed harvest

Serial harvests of plants began 7 d after 50% anthesis and continued at 5 d intervals until well after the developmental stage when the seed crop would have been harvested traditionally. Each harvest comprised all the plants from between four and eight pots; plants grown in the pots on the outside of the rows were treated as discards; after sufficient pots had been removed for a given harvest, the discard pots were replaced in position in order to maintain the discard area around the seed 'crops'.

Panicle and seed colour were recorded, the seeds then threshed gently by hand, and empty seeds removed. Samples of 200 seeds each were withdrawn for initial determinations of moisture content and germination, while the remaining seeds were dried to 10–14% moisture content (wet basis) in

TABLE 2. *Durations from sowing to 50% anthesis and from 50% anthesis to the end of the seed-filling phase (mass maturity), rate of seed-filling and final mean seed dry weight for three cultivars of rice grown in two temperature regimes*

		Cultivar		
	Regime	Taipei 309	Intan	Ketan Amnera
Sowing to 50%	28/20 °C	109	104	119
anthesis, d	32/24 °C	107	82	97
50% anthesis to	28/20 °C	19·6 (0·49)	19·2 (1·25)	20·4 (1·29)
mass maturity, d (s.e.)	32/24 °C	18·8 (0·49)	17·9 (0·32)	18·0 (0·52)
Rate of seed filling*,	28/20 °C	1·01 (0·035)	1·28 (0·120)	1·16 (0·111)
mg (s.e.) d^{-1}	32/24 °C	1·07 (0·038)	1·44 (0·034)	1·27 (0·049)
Final mean seed	28/20 °C	17·5 (0·14)	20·0 (0·19)	25·7 (0·21)
dry weight, mg (s.e.)	32/24 °C	17·6 (0·15)	20·0 (0·12)	24·4 (0·13)

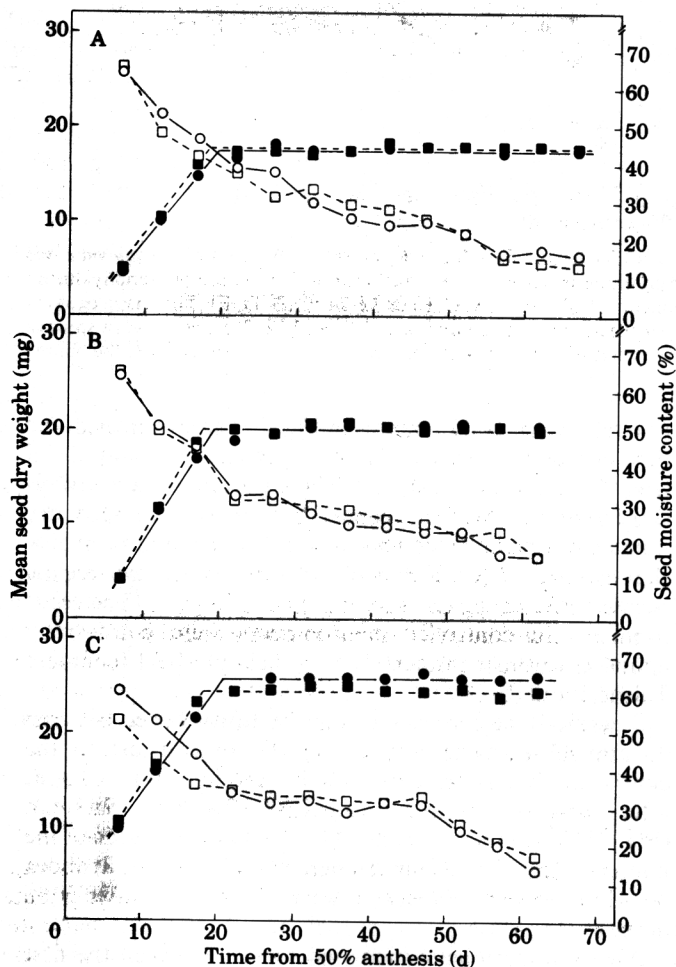* Determined between 7 and 17 d after 50% anthesis.

FIG. 1. Mean seed dry weight (solid symbols) and moisture content (open symbols) of seeds of the *japonica* rice cv. Taipei 309 (A), the non-glutinous *indica* rice cv. Intan (B), and the glutinous *indica* rice cv. Ketan Amnera (C) harvested serially during seed development and maturation from plants grown in controlled environments of 32/24 °C (squares) and 28/20 °C (circles). The end of the seed-filling phase (mass maturity) is denoted by the intersection between the continuous lines for the cooler regime and the broken lines for the warmer regime.

a drying cabinet maintained at 15–17 °C with 12–15% relative humidity. Each seed sample was then stored hermetically at 3–5 °C for 3–5 d (in order to allow moisture to equilibrate within and among the seeds). Equilibrium relative humidity was then determined at 20 °C, using a Humidat IC1, and drying resumed if this value was > 70%. Once dried, a further sample of 200 seeds was drawn for a germination test and the remaining sample stored hermetically at −20 °C.

Seed moisture contents were determined using the high-constant-temperature oven method (International Seed Testing Association, 1985a, b), the only variation being that 2 × 100-seed samples were used in place of 2 × 4–5 g samples in each case. The two-stage method (International Seed Testing Association, 1985a, b) was used for moist seeds.

Seeds were tested for germination between moist rolled paper towels in the alternating temperature regime of 34/11 °C (16h/8 h) recommended by Ellis, Hong and Roberts (1983), for 28 d initially. The seed covering structures (glumes, lemmas and paleas) of firm, ungerminated seeds were then removed and the germination test continued until these seeds germinated (often within a further 7 d, but in the most dormant seeds a much longer duration, sometimes combined with further surgical treatment, was required to promote germination).

Determination of potential longevity

The first and last seed samples were harvested on 20 Jul. and 13 Oct. 1992, respectively; the determination of potential longevity began on 30 Nov. 1992 (cv. Ketan Amnera), 9 Dec. 1992 (cv. Intan), and 4 Jan. 1993 (cv. Taipei 309), the seeds having been stored hermetically at −20 °C subsequent to drying to 10–14% moisture content. Seeds were withdrawn from storage and held sealed overnight at 20 °C before opening the packets.

The moisture content of each sample was adjusted to 15% (±0·2%) by humidification above water at 20 °C (for between 2 and 24 h, depending upon initial moisture content). The seeds were then stored hermetically at 3–5 °C for 5 d, and a sample then withdrawn for moisture content determination. For each of the 74 seed lots, 10–14 samples of 120–200 seeds (depending upon total sample size) were
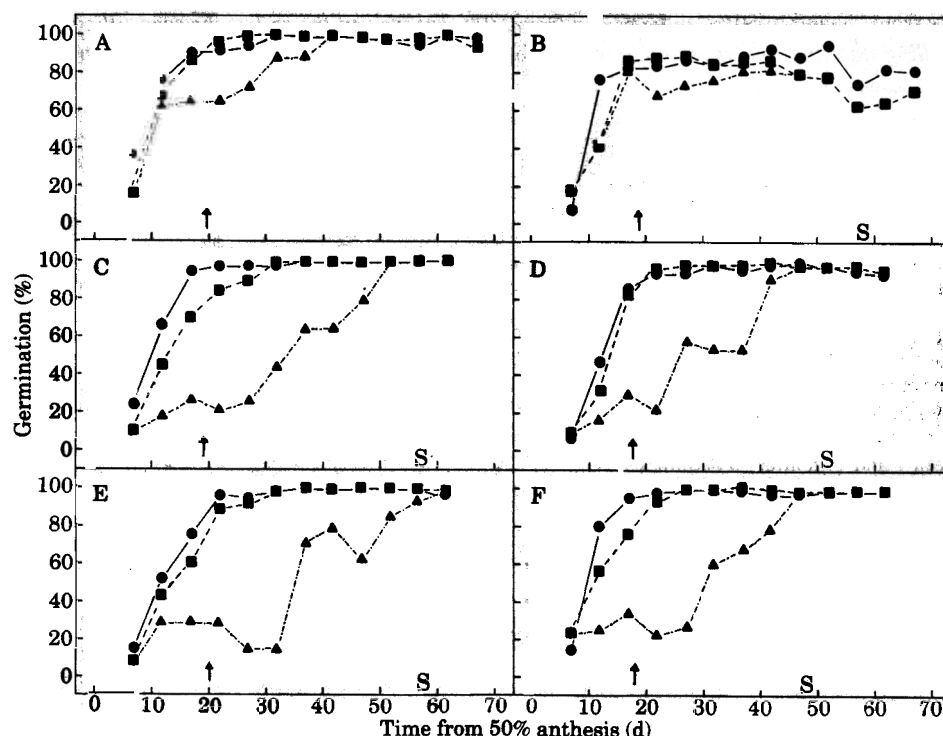
FIG. 2. Changes in ability to germinate normally in standard tests at 34/11 °C for freshly-harvested (●) or dried (■) seeds of the *japonica* rice cv. Taipei 309 (A, B), the non-glutinous *indica* rice cv. Intan (C, D), and the glutinous *indica* rice cv. Ketan Amnera (E, F) harvested serially during seed development and maturation from plants grown in controlled environments of 28/20 °C (A, C, E) or 32/24 °C (B, D, F). The triangles show the interim results for dried seeds after 28 d in test but before the removal of the seed covering structures. Hence the difference between squares and triangles is indicative of the degree of dormancy. The arrows indicate mass maturity; S indicates when seeds began to be shed from the plants.

sealed in separate laminated aluminium foil bags. These were then stored on the same shelf (within each cultivar) of an incubator maintained at 40 °C (± 0.5 °C). Samples were removed for germination tests at regular intervals for up to 39 d for the *japonica* seed lots and for up to 49 d for the *indica* seed lots. The longevity of the three seed lots provided by IRRI (Table 1) was also determined at 40 °C with 15% moisture content.

Given that, within each tunnel, the three cultivars had been grown as three separate seed 'crops', and that the subsequent laboratory work was staggered slightly, the results for seed survival during storage were analysed separately for each cultivar. Seed survival curves were fitted to the data in accordance with eqn (1) by probit analysis using GLIM, in which analyses the criterion of survival was the ability of a seed to produce a normal seedling (International Seed Testing Association, 1985 *a*, *b*).

RESULTS

Plants of cv. Intan reached 50% anthesis soonest in both environments, and progress to flowering was more rapid in the warmer than the cooler regime in all three cultivars (Table 2). However, in cv. Taipei 309 this difference in duration was negligible (thereby indicating that the optimum temperature for rate of floral development is coolest in this cultivar). The durations from 50% anthesis to mass maturity were determined by an objective iterative regression analysis procedure (Pieta Filho and Ellis, 1991 *a*) with the observa-

tions shown by solid symbols in Fig. 1. The estimates of the time of mass maturity varied only between 17·9 and 20·4 d from 50% anthesis (Table 2). These durations were always shorter in the warmer regime, but final mean seed dry weights were unaffected (cvs Taipei 309 and Intan) or only slightly reduced (cv. Ketan Amnera) in the warmer regime because seed-filling rates were greater (Table 2). The seeds produced in controlled environments were consistently lighter than those produced in the field at IRRI (compare Tables 1 and 2).

Seed moisture contents at mass maturity varied between 36 and 43% (mean 40%) (Fig. 1). In contrast to the consistent, but slow, reduction in seed moisture content after mass maturity in cvs Taipei 309 (Fig. 1 A) and Intan (Fig. 1 B), the moisture content of the maturing seeds of the glutinous *indica* cv. Ketan Amnera remained stable at about 30–33% moisture content between 27 and 47 d after 50% anthesis (Fig. 1 C).

Ability to germinate increased rapidly between the first and fourth harvests, with comparatively few (typically no more than 20%) of the seeds capable of germinating normally being damaged by desiccation to 10–14% moisture content (Fig. 2). Dormancy (compare triangles and squares in Fig. 2) was often considerable in early harvests, was reduced during seed development and maturation, was reduced in the warmer compared to the cooler seed production regime, and was least in the *japonica* cultivar.

The majority of the seeds harvested 2–4 d after mass maturity (i.e., 22 d after 50% anthesis) were capable of
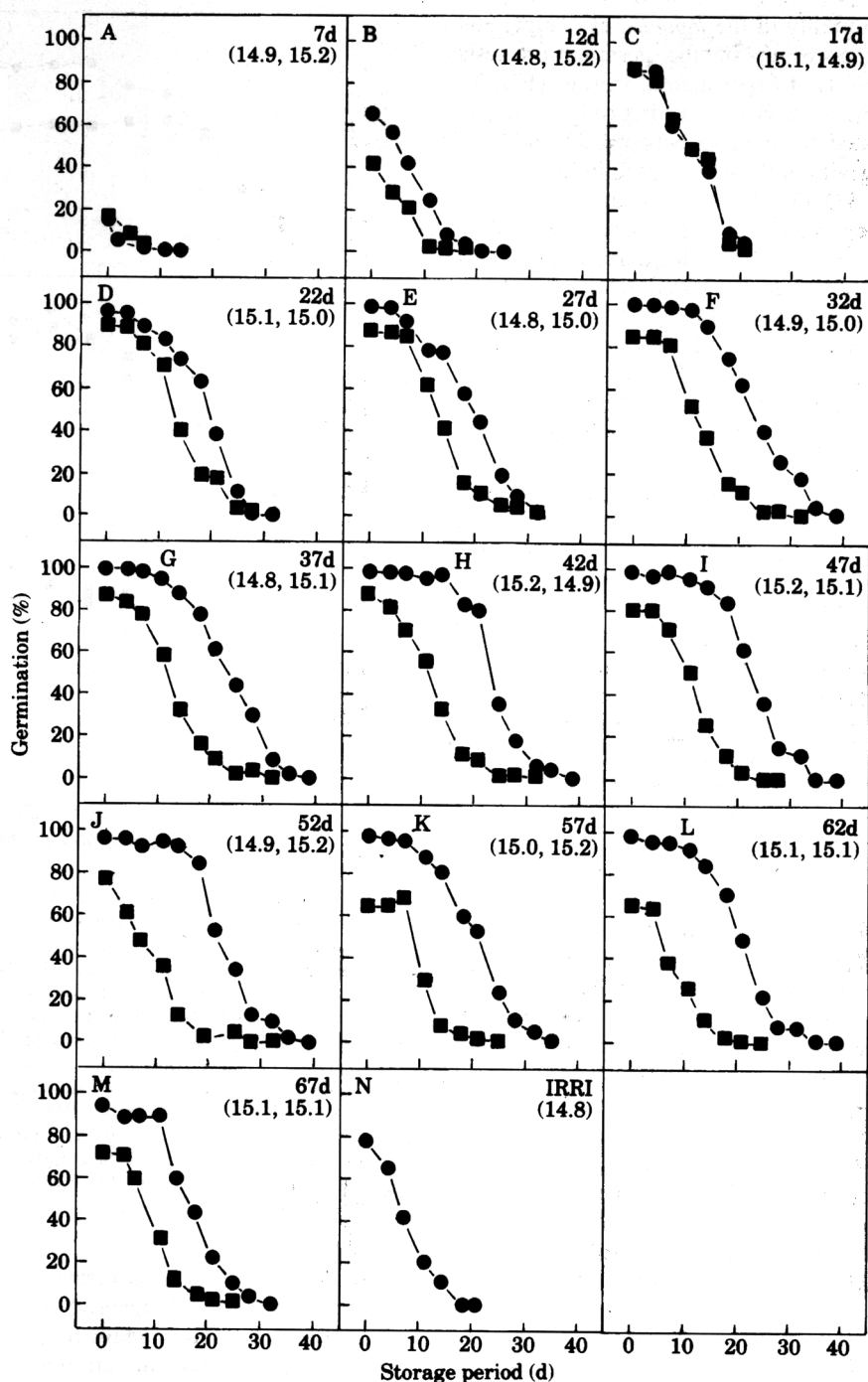
FIG. 3. Seed survival curves (% normal germination plotted against period of experimental storage at 40 °C) for the *japonica* rice cv. Taipei 309 harvested serially during seed development and maturation from plants grown in controlled environments of 28/20 °C (●) or 32/24 °C (■) at Reading (A—M). Seeds were stored hermetically in laminated aluminium foil bags at about 15% moisture content (values in parentheses show the actual seed storage moisture contents for seeds produced in the cooler and warmer regimes, respectively). The durations shown in (A—M) are those from 50% anthesis to harvest. The survival curve for the original seed lot produced at IRRI (Table 1) is shown in (N).

producing normal seedlings in standard germination tests, and most of these were also capable of surviving desiccation to 10–14% moisture content. Nevertheless, the maximum ability to germinate following desiccation was not attained until 27–37 d after 50% anthesis (i.e., 8–18 d after mass maturity). However, whereas in most combinations of cultivar and seed production temperature regime 99–100% normal germination was ultimately achieved, the maximum germination of dried seeds of cv. Taipei 309 produced in the warmer regime was considerably less and never exceeded 90% (Fig. 2B).

This large effect of the temperature of the seed production

environment on seed quality in the *japonica* cv. Taipei 309 was confirmed by the results of the germination tests following various periods of experimental storage (Fig. 3). Moreover, whereas the longevity of seeds produced in the cooler regime continued to increase between 22 and 37 d after anthesis the longevity of those produced in the warmer regime did not (Fig. 3 D–G). Also shown in Fig. 3 is the survival curve of the original seed lot produced at Los Baños in the Philippines (Fig. 3 N). This curve (Fig. 3 N) is similar to that for the seeds harvested 62 d after 50 % anthesis in the warmer regime (Fig. 3 L) or 12 d after anthesis in the cooler regime (Fig. 3 B). Note that the slopes of the survival curves for the IRRI seed lot is similar to that for all 26 seed lots produced at Reading. A similar pattern was detected in the seed survival curves for the other two cultivars (data not shown).

The results for normal germination during experimental storage were analysed by probit analysis in accordance with eqn (1) within each cultivar separately. Those analyses confirmed that, within each of the three cultivars, neither the time of seed harvest nor the temperature of the seed production regime (nor the interaction between these two factors) influenced the slope of the seed survival curves during storage ($P > 0.25$)—and so the value of σ of eqn (1) did not vary, whereas the effect of seed harvest date and the interaction between this factor and the temperature regime influenced potential longevity [K_i, eqn (1)] significantly ($P < 0.005$); i.e., these factors displaced the seed survival curves in time and therefore affected the longevity of all seeds within each population. One interesting difference between the *japonica* cv. Taipei 309 on the one hand and the two *indica* cultivars on the other, was that the main effect of the temperature of the seed production environment (on potential longevity) was significant for the former ($P < 0.005$) but not for the latter ($P > 0.25$).

The resultant estimates of K_i show that potential longevity continued to increase subsequent to mass maturity in all three cultivars (Fig. 4). However, whereas this continuing trend was apparent in both temperature regimes for the two *indica* cultivars (Fig. 4 B and C), it was only apparent in the cooler regime for the *japonica* cultivar (circles in Fig. 4 A); in the warmer regime, the greatest potential longevity of cv. Taipei 309 was shown by seeds harvested on the first occasion after mass maturity (i.e., 22 d after 50 % anthesis, squares in Fig. 4 A). In the cooler regime, the maximum potential longevity of this cultivar was attained 32 d after 50 % anthesis, or 12 d after mass maturity. For cv. Intan, maximum potential longevity was attained 37 d after 50 % anthesis in the cooler regime and 47 d after 50 % anthesis in the warmer regime. However, in the latter case the difference between the estimates of K_i for 37 d and 47 d after 50 % anthesis was marginal (Fig. 4 B), and so it can be assumed that maximum potential longevity was first attained some 18–19 d after mass maturity in both regimes. And similarly in the glutinous *indica* cv. Ketan Amnera; maximum potential longevity was first attained 37 d after 50 % anthesis, or 17–19 d after mass maturity, in both temperature regimes (Fig. 4 C).

The decline in potential longevity on the mother plant, subsequent to the achievement of maximal values, was
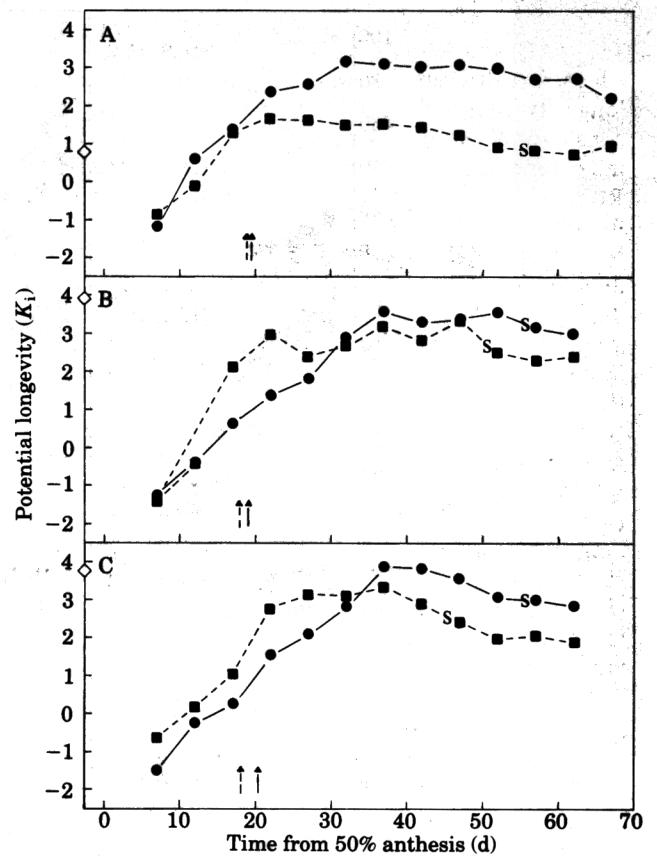

FIG. 4. Changes in the potential air-dry seed storage longevity [estimate of the seed lot constant K_i of the seed viability equation, eqn (1)] of seeds of the *japonica* rice cv. Taipei 309 (A), the non-glutinous *indica* rice cv. Intan (B), and the glutinous *indica* rice cv. Ketan Amnera (C) during seed development and maturation in controlled environments of 28/20 °C (circles) or 32/24 °C (squares) at Reading. The solid and broken arrows indicate mass maturity (cooler and warmer regimes, respectively). Seeds were stored hermetically at 40 °C (± 0.5 °C) and 15 % (± 0.2 %) moisture content (wet basis); within each of the three cultivars the seed survival curves had common slopes ($1/\sigma$) of (A) -0.135 (s.e. 0.0011), (B) -0.131 (s.e. 0.0015), (C) -0.119 (s.e. 0.0012) and hence the estimates of σ were (A) 7.4 d, (B) 7.6 d, (C) 8.4 d. The diamonds on the *y*-axis indicate the equivalent value for the potential longevity of the seed lots produced at Los Baños, Philippines (Table 1); S indicates when seeds began to be shed from the plants.

comparatively slow (in contrast to the earlier rates of increase in potential longevity) and was greatest in the glutinous *indica* cv. Ketan Amnera (Fig. 4 C). This may have been because seed moisture contents of cv. Ketan Amnera during this period were somewhat greater than those in the other two cultivars (Fig. 1)—related possibly to different hygroscopic characteristics of the endosperm.

Within all three cultivars, the greatest maximum potential longevity was attained in the cooler seed production environment. Moreover, K_i was always greater in the cooler than in the warmer regime when seed harvest was delayed after maximum potential longevity had been attained. Finally, whereas the quality of the seedlots of the two *indica* cultivars produced at Los Baños were as good as the best quality seed lots produced in controlled environments at Reading (Fig. 4 B, C), that for the *japonica* cv. Taipei 309 was very much poorer (Fig. 4 A).

DISCUSSION

There are theoretical reasons for arguing that potential longevity (quantified here by the value of the seed lot constant, K_i, of the seed viability equation) is a good indicator of seed quality and vigour in many crops (Ellis and Roberts, 1980b, 1981). Moreover, in long-term seed stores for plant genetic resources conservation (i.e., seed gene-banks) potential longevity is the criterion of seed quality of direct concern. The results presented here for the changes during seed development and maturation in the potential longevity of seeds of the two *indica* rice cultivars produced in both temperature regimes and for those of the *japonica* rice cultivar produced in the cooler regime (Fig. 4) are in general agreement with the results of earlier studies in other crops (Kameswara Rao et al., 1991; Pieta Filho and Ellis, 1991a; Demir and Ellis, 1992a, b, 1993; Ellis and Pieta Filho, 1992; Zanakis et al., 1994): maximum potential longevity was not attained until some time (12–19 d) after mass maturity. Hence, these results contradict the hypothesis (Harrington, 1972) that maximum seed quality is attained at the end of the seed-filling phase and that viability and vigour then decline. In contrast, the results for the *japonica* cultivar produced in the warmer regime do satisfy the first part of the above hypothesis, although the reduction in K_i values consequent upon delaying seed harvests for 15 d beyond mass maturity was negligible (squares in Fig. 4A) and the germination capacity of freshly-harvested seeds showed no decline at all in the 33 d after mass maturity (circles in Fig. 2B).

It has long been recognised that high seed production temperatures can be deleterious to seed quality; for example, this has been documented in soyabean [*Glycine max* (L.) Merrill] (Green et al., 1965; TeKrony et al., 1980). At first sight, the effect of the temperature of the seed production regime on the changes in rice seed quality during development and maturation appear inconsistent between the *japonica* cultivar and the two *indica* cultivars (Fig. 4). However, in all three cultivars it can be seen that a deleterious effect of the higher temperature seed production environment on seed quality is detectable, but not until after mass maturity. In particular, the increase in K_i values subsequent to 22 d after 50% anthesis (the first seed harvest after mass maturity) is similar for the two *indica* cultivars and very much less for seeds produced in the warmer than the cooler regime, *viz* 0·4 (cv. Intan), 0·6 (cv. Ketan Amnera), 2·2 (cv. Intan) and 2·3 (cv. Ketan Amnera) respectively (Fig. 4B, C).

This observation was tested by analysing the trend of the estimates of K_i with time from mass maturity. These analyses showed that, between 22 and 37 d after 50% anthesis, K_i increased significantly ($P < 0.005$) with a significant difference between the two temperature regimes in the rate of change ($P < 0.005$), but with no difference in this rate between the two *indica* cultivars within each regime ($P > 0.10$); the increase was only 0·025 d^{-1} (s.e. 0·0097) in the warmer regime, but 0·154 d^{-1} (s.e. 0·0105) in the cooler regime (i.e., six times greater, or an absolute difference of 0·129 d^{-1}). In this sense then, the difference between the two temperature regimes had a roughly consistent effect on the

change in K_i values with time from mass maturity in all three cultivars; however, because the rate of increase in the *japonica* cultivar in the cooler regime (0·077 d^{-1}, s.e. 0·0270) was only half that in the two *indica* cultivars, the effect of the increase in the temperature of the seed production regime for the *japonica* cultivar was to result in a negative trend of K_i values after mass maturity (-0.012 d^{-1}, s.e. 0·0018). Indeed, in this cultivar the effect of the increase in seed production environment temperature reduced the post mass maturity trend in K_i values by *only* 0·089 d^{-1}; in this sense, it could be argued that seed quality in cv. Taipei 309 (though poorer overall) was in fact slightly less sensitive to the increase in seed production temperature imposed here than the two *indica* cultivars.

The demonstration here that this effect of increase in temperature is sufficient in the *japonica* rice cv. Taipei 309 to influence the stage during seed development and maturation when seeds attain maximum quality (Fig. 4A) may provide an explanation for the contradictory conclusions reached between certain seed quality development studies in other crops. This is particularly so in soyabean in which crop research in the USA has provided results which supported the Harrington hypothesis (TeKrony et al., 1980), whereas UK research (probably at cooler temperatures) showed that maximum potential longevity was not attained until some time after mass maturity (Zanakis et al., 1994). Whether or not the above speculation is valid remains to be seen. However, it is clear that a hot seed production environment can bring forward to an earlier developmental stage the time at which maximum seed quality is attained (Fig. 4A), or (in less vulnerable cultivars) it reduces the improvement in seed quality that occurs subsequent to mass maturity (Fig. 4B, C). This demonstration provides an opportunity to researchers investigating the biochemical basis of seed quality to break the association between seed development, maturation and seed quality.

The general comments of Chang (1991) that *japonica* rice cultivars show poorer longevity than *indica* rice cultivars are supported by these results. Even in the cooler seed production regime, the maximum potential longevity of the *japonica* cultivar was slightly less than that of the two *indica* cultivars, while the estimate of σ was also marginally briefer (Fig. 4). Nevertheless, the magnitude of the difference in longevity between *japonica* and *indica* cultivars reported by Chang (1991) may have resulted from the natural seed production environment at Los Baños being too warm for the *japonica* accessions as compared with the *indica* (and *javanica*) rice accessions.

The genebank at IRRI currently holds more than 80000 accessions—of which about 8% are *japonica* rices. At present, but only when necessary, all accessions are regenerated in the field at IRRI. Now, although the research reported here was limited to a single *japonica* cultivar, it implies that the seed production environment at IRRI may be too harsh for *japonica* cultivars and that, in so far as seed accessions for the IRRI genebank are concerned, *japonica* accessions might be better regenerated in a cooler environment. Such seed is likely to remain viable more than three times as long as that produced at Los Baños (assuming a regeneration standard of 85%). Clearly, further research

with a wide range of *japonica* accessions is required to confirm this implication. Since upland *javanica* cultivars belong to the same isozyme polymorphism group (VI) as the classical *japonica* rices (Glaszmann, 1986), it would also be helpful to include upland *javanica* rice cultivars in further research.

Finally, the results presented here provide additional support to the conclusion of Roberts (1963), from an elegant investigation in six cultivars of rice, that while dormancy and longevity may often be positively correlated the relation is not causal. For example, comparison between Figs 2C and 4B shows that from 22 to 37 d after 50 % anthesis dormancy was reduced whereas potential longevity increased for cv. Intan in the cooler regime and, moreover, that from 37 to 52 d after 50 % anthesis the decline in dormancy continued whereas no further change in potential longevity occurred.

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