

Germination and early seedling growth in some northern wild rice (*Zizania palustris*) populations differing in seed size

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A field survey of eight northern *Zizania palustris* populations indicated that there is substantial variation in seed size. Variability is partitioned approximately equally among populations and among individuals within populations. Germination dynamics and temperature sensitivity of germination differed among four populations tested, but the differences were not apparently related to mean population seed size. Mean population seed size did appear to influence the germinability of viable seeds, such that a greater proportion of larger seeds exhibited prolonged dormancy. In a test using three populations differing in mean seed size, those with large seeds produced larger seedlings than populations characterized by small seeds. It appears that in *Z. palustris* seed size influences whether or not a viable seed will germinate and the size of the resulting seedling, but not the rate at which germinable seeds are recruited to form a seedling population.

Key words: *Zizania*, seed size, germination.

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L'observation au champ de huit populations de *Zizania palustris* indique qu'il y a une importante variation dans la dimension des graines. La variabilité se répartie presque également entre les populations et entre les individus. La dynamique de germination et la sensibilité de la germination à la température diffèrent entre quatre populations expérimentées, mais les différences ne semblent pas reliées à la grosseur moyenne des graines de la population. La grosseur moyenne des graines de la population semble cependant influencer la germinabilité des graines viables, de sorte qu'une plus forte proportion des grosses graines montrent une dormance prolongée. Dans un essai faisant appel à trois populations qui diffèrent par la grosseur moyenne des graines, celles possédant de grosses graines ont produit des plantules plus robustes que celles provenant de populations graines influence si une graine viable va germer ou non ainsi que la grosseur de la plantule qui en résulte, mais n'affecte pas le taux à lequel les graines capables de germer sont mises ensemble pour former une population.

Mots clés : *Zizania*, grosseur des graines, germination.

[Traduit par la rédaction]

Introduction

The "fitness" of an individual is a function of its relative ability to contribute its genes to populations in subsequent generations. Broadly speaking, then, fitness has two components: the number of offspring produced, and the "quality" or relative ability of those offspring to survive and reproduce themselves. Plant fitness has traditionally been estimated as a function of seed production, especially seed number (Primack and Kang 1989). However, the size of offspring (i.e., the amount of maternal resource investment they represent) may influence their early growth and development. For example, seed size has been found to affect germination rates and percentages, the range of conditions permitting germination, and seedling size (Schaal 1984; Stanton 1984; Winn 1985; Wulff 1986a; Marshall 1986; McGinley et al. 1987; Roach and Wulff 1987; Kalisz 1989). Because larger offspring may have an initial competitive advantage that ultimately translates into greater reproductive success, the relative size of its offspring may be an important component of the fitness of an individual plant.

Northern wild rice (*Zizania palustris*) is an annual aquatic grass that is widespread in the central and eastern regions of southern Canada and the adjacent United States. The plant is monocious and protogynous, and reproduces exclusively by

ypopsis or grain, which will be hereafter referred to as a seed. The large edible seeds of *Z. palustris* have been harvested as a food crop by both indigenous and immigrant peoples in the Great Lakes basin for generations. Casual observation indicates that there is considerable variability in seed size among and within northern wild rice populations. However, the extent and structure of this variability and its consequences during early development have not been ascertained. This paper describes a series of studies that were undertaken first to quantify the extent and structure of variability in seed size in some northern *Z. palustris* populations, and second to compare germination dynamics and seedling size for populations differing in seed size.

Materials and methods

Structure of variation in seed size

Seed from eight wild rice populations was used in these experiments. The particular seed lots used varied in different experiments, depending on availability and the purpose of the particular study. Table 1 lists the locations of the source populations. All statistical tests were performed using Statgraphics 3.0 (Statistical Graphics Corp. 1988) or SPSS-X (SPSS Inc. 1988) computer software.

Fresh seed weight served as the measure of size. Seeds were blotted dry and the awns removed before weights were determined. Lemmas and paleas were left intact. For the initial survey of size variability,

TABLE 1. Locations of seed source populations used in various studies

Population ^a	Lat. N	Long. W	Among-population variability	Germination dynamics	Seedling size
RL	51°13'	93°03'	×	×	×
GN	49°35'	91°45'	×	×	×
S	55°05'	105°30'	×	×	×
WF	49°32'	91°15'	×	×	×
RI	49°45'	91°22'	×	×	×
ER	49°29'	91°32'	×	×	×
V	50°50'	90°08'	×	×	×
CH	49°41'	91°19'	×	×	×

^aCH, Chamock Lake; ER, English River; GN, Grassy Narrows; RI, Rice Lake; RL, Red Lake; S, Sikachu Lake; V, Velos Lake; WF, Whitefish Lake.

weights were obtained for 200 seeds selected at random from bulked samples collected in eight diverse wild rice populations (see Table 1). Summary statistics were obtained for each population, and an analysis of variance (ANOVA) was carried out to partition variability within and among populations. Percent variance was calculated on the basis of expected mean squares (Sokal and Rohlf 1981, p. 216). Cochran's C-statistics were computed concurrently with all ANOVAs to test for heterogeneity of variance. Duncan's multiple range test was used to identify groups of populations with significantly different mean fresh seed weights; these groups are referred to as different size classes.

To partition variability within and among plants within a population, an ANOVA was performed on a data set consisting of weights of 10 seeds from each of 17 cultivated plants. Plants were grown in tubs suspended from rafts to a depth of 1 m below the surface of Back Lake, a small pond near Thunder Bay, Ontario (see Stevenson and Lee 1987 and Counts and Lee 1988 for further details regarding raft cultivation). The soil was treated with slow-release fertilizer at a rate of 200 kg N ha⁻¹.

Several analyses were carried out to demonstrate that fresh seed weight is an appropriate measure of seed size and that it is an indicator of maternal provisioning of the embryo. To relate fresh weight to other size indicators, lengths and widths (at the widest point) were measured in addition to fresh weights for 350 seeds collected from 53 plants (5–10 seeds per plant) cultivated on rafts (see above). After these measurements were taken, seeds were dried in an 80°C oven for 24 h and then reweighed. The correlation (Pearson coefficient) between fresh and dry seed weight was computed, and a regression analysis on fresh weight was performed using length and width as predictor variables.

To establish that higher total grain weight indicates greater maternal provisioning of the embryo, a series of weights was obtained for each of 120 seeds selected at random from bulk collections from four field populations. The four populations were chosen to represent the range of average seed sizes. Individual seeds were scored for total grain weight (grain with hull intact, awn removed); seed weight (grain with hull removed), and endosperm weight (embryo and hull removed, but includes pericarp). Embryo and hull weights were obtained by subtraction. Principal components analysis (PCA) was used to describe the interrelations between total grain weight and its component (hull, endosperm, and embryo) weights.

Germination dynamics

Seed from four populations representing large (Rice Lake, population 4), small (Whitefish Lake, population 1), and intermediate (Red Lake, population 2; Sikachu Lake, population 3) size classes was used. For each population, three lots of 125 after-ripened (4°C for 7–8 months) seeds were placed in Petri dishes, covered with tap water, and then placed in growth chambers with a 16-h photoperiod and a diurnally fluctuating high (25:15°C) or low (15:5°C) temperature regime. These regimes are optimal and suboptimal for germination, respectively, according to Atkins et al. (1987). Germination was monitored for 2 weeks. Seeds were considered germinated when the coleoptile had completely lifted away from the hull. Those that failed

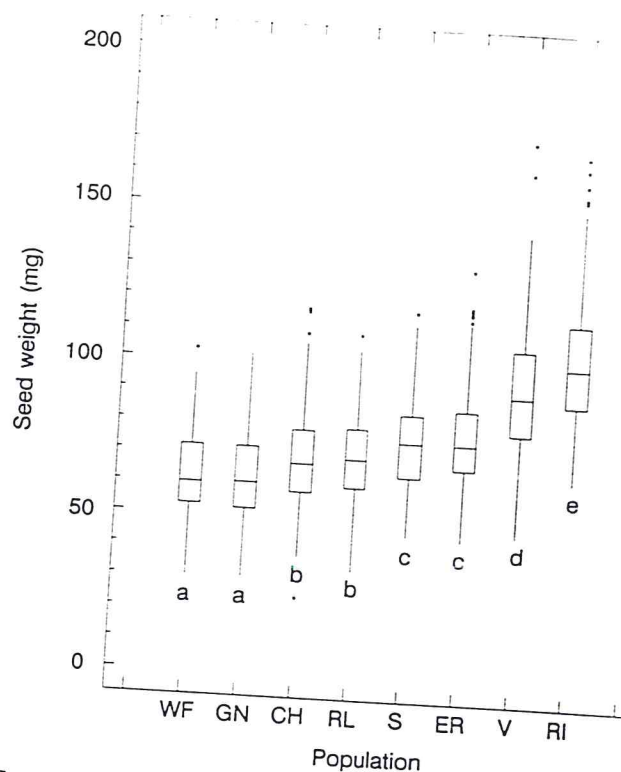


FIG. 1. Box and whisker plots of fresh seed weight for eight northern wild rice populations. Horizontal lines bisect boxes at the median and the limits of the boxes define the lower to upper quartile interval. Whiskers extend to 1.5 times the interquartile range, with outliers beyond this range shown as points. Boxes identified with different letters represent significantly different ($p < 0.05$) mean values according to Duncan's multiple range test. Populations as in Table 1.

to germinate were stored in the dark at 4°C and reexamined after 2½ months; all that failed to germinate during this period were tested for viability using the tetrazolium chloride (TTC) test (Moore 1973; 0.1% TTC for 4–5 h at 30°C). Germination was expressed in two ways: as a percentage of viable seeds (total germination) and as a percentage of seeds that germinated during the experiment (proportional germination).

Analyses of covariance (ANCOVAs) of log-transformed data were used to assess the effects of population and environmental regime on germination rates. The log transformation was used to linearize the germination curve. Proportional germination was analyzed with days as the covariate and temperature and population as the factors. The subroutine MANOVA of SPSS-X was used for this procedure (SPSS Inc. 1988, pp. 617–619), with stepwise analyses to assess interaction terms and to test the assumption of homogeneous slopes. In a second set of analyses the (i) two temperature regimes and (ii) four populations were considered separately to fit separate regression lines for each population within a regime, or for each regime for a population. Total germination was analyzed using a simple two-way ANOVA with temperature regime and population as factors.

Seedling size

After-ripened bulk seed from three populations representing small (Whitefish Lake, population 1), medium (Red Lake, population 2) and large (Velos Lake, population 3) size classes was germinated in tubs in a greenhouse with a 16-h photoperiod and a diurnal temperature regime of approximately 25:15°C. After 7 days, the number of leaves, number of roots, and maximum width of the second leaf were determined for 20 seedlings from each population. The seedlings were then excised and weighed fresh and after drying at 80°C for 2 days. Fresh weights of the seed remaining after seedling excision (residual

TABLE 2. Summary statistics of 200 fresh seed weights measured for each of eight northern wild rice populations

Population	Mean (mg)	SD	Min.	Max.	Interquartile range	Skewness	Kurtosis
WF	62.2	13.2	30.0	103.0	19.0	0.283	-0.188
GN	62.4	14.4	30.0	102.0	20.0	0.374	-0.102
CH	68.9	15.4	24.0	117.0	20.0	0.479	0.470
RL	69.8	14.3	33.0	109.0	19.0	0.136	-0.280
S	75.2	14.0	45.0	117.0	20.0	0.389	-0.097
ER	77.5	15.8	44.0	131.0	19.0	0.645	0.519
V	93.7	21.4	46.0	173.0	27.0	0.622	0.604
RI	103.7	20.5	64.0	169.0	26.0	0.772	0.447

NOTE: Populations as in Table 1.

TABLE 3. Analyses of variance of fresh seed weight among eight populations and among plants within a single population of wild rice

Source of variation	df	MS	F
Among populations ^a			
Among populations	7	0.0446	166.18***
Within populations	1615	0.0003	
Within populations ^b			
Among individuals	16	2705.18	52.2***
Within individuals	153	51.82	

NOTE: ***, $p < 0.001$.
Cochran's $C = 0.2124$; $p = 0.000$.
Cochran's $C = 0.111$; $p = 0.740$.

TABLE 4. Principal components analysis of total and partitioned seed weight for 120 seeds from four wild rice populations differing in mean seed size

Component	Standardized variable weights				% variance explained
	Total	Endosperm	Hull	Embryo	
1	0.601	0.579	0.526	-0.162	68.40
2	0.038	-0.037	-0.297	0.953	25.15
3	-0.197	-0.560	0.772	0.226	6.45

seed weight) were also obtained. For all variables except leaf number, ANOVAS were carried out using the SPSS-X subroutine ONEWAY, and variance components calculated on the basis of expected mean squares. Specific means were compared a priori by the use of contrast statements. A Kolmogorov-Smirnov test indicated that leaf number was not normally distributed, so a nonparametric Kruskal-Wallis ANOVA was used for this variable.

Results

Structure of variation in seed size

There was significant variation in fresh seed weight for eight northern wild rice populations; population means ranged from 62 to 104 mg/seed, and the overall range in seed weight was 24-173 mg (Fig. 1; Table 2). Although there were significant differences among populations for fresh seed weight ($F_{7,1615} = 166.18$), more than half (57%) of the total variation in fresh seed weight occurred within populations (Table 3). The significant Cochran's C -statistic showed that variances were heterogeneous among populations; populations with highest mean seed weights were also the most variable (Fig. 1). Seed weights were also positively skewed and somewhat kurtotic in the populations with the highest mean values.

Analysis of variation in a single population indicated that the majority of the variance (84%) could be attributed to the

TABLE 5. Stepwise analysis of covariance for proportional germination in four wild rice populations, differing in mean seed size, subjected to two temperature regimes

Source of variation	df	MS	F
Step I			
Covariate (days)	1	0.98	299.1***
Constant	1	0.82	213.0***
Temperature (T)	1	1.86	484.3***
Population (P)	3	0.01	3.2*
P × T	3	0.01	3.4*
Within cells	183	0.004	
Step II			
Covariate (days)	1	4.98	1295.0***
Constant	1	0.82	212.4***
Temperature (T)	1	1.86	482.8***
Population (P)	3	0.01	3.2*
P × T × days	3	0.01	3.2*
Within cells	183	0.004	

NOTE: *, $p < 0.05$; ***, $p < 0.001$.

among-plant component ($F_{16,153} = 51.82$). Means for individual plants varied from 41 to 95 mg. Variances among plants were homogeneous, as shown by the nonsignificant Cochran's C . If one assumes that this population is typical, variability in fresh seed weight is partitioned approximately equally among populations (43%) and among individual plants within populations ($0.57 \times 0.84 = 0.48$, or 48%).

The regression of fresh seed weight on seed length and width had a multiple R^2 of 0.880 (Fig. 2), indicating that fresh seed weight is a reasonable indicator of overall seed size. Each of the dimensional variables alone was significantly ($p \leq 0.01$) correlated with fresh weight as well but had relatively poor explanatory power (R^2 for width vs. weight was 0.605, and for length vs. weight was 0.399).

The high correlation between fresh and dry grain weights ($R^2 = 0.894$, $p \leq 0.01$) demonstrated that an increase in seed mass does not reflect a proportionally higher water content. PCA indicated that fresh seed weight is, however, a good indicator of maternal provisioning of the embryo. Three principal components (PCs) accounted for all the variation in the data set (Table 4). The first component, accounting for 68.4% of the variation, was primarily a function of total weight and endosperm weight, although hull weight also made an important contribution (Table 4). Both total weight and endosperm weight made very minor contributions to the second PC, which was mainly a function of embryo weight and accounted for 25.15% of the total variance. The weighting of variables on the first two components illustrated in Fig. 3 shows that total

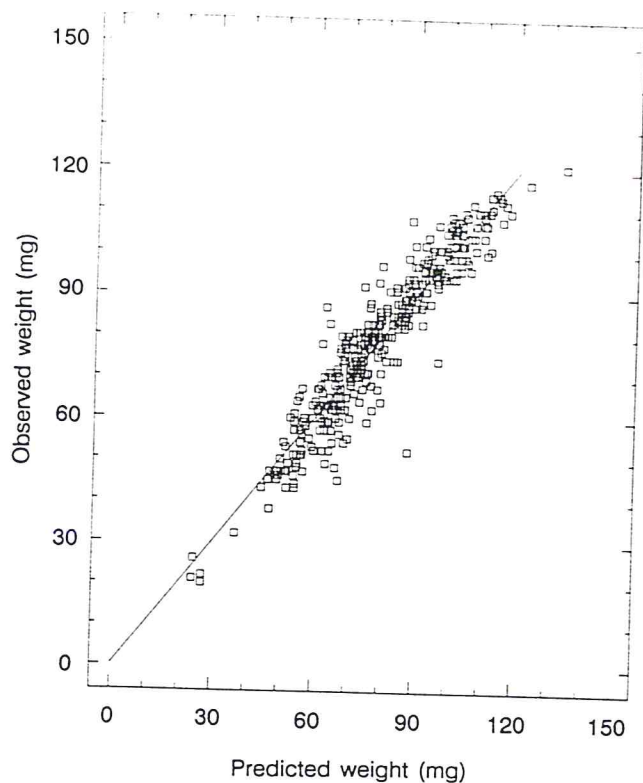


FIG. 2. Predicted vs. observed fresh weights of 350 wild rice seeds from 53 plants from a single population. Predicted values were obtained using the regression equation $y = -122.15 + 48.79(\text{seed length}) + 445.06(\text{seed width})$. Both partial regression coefficients and the intercept were significant, with $p < 0.001$. The multiple R^2 for the model was 0.880. The line shown has a slope = 1, as would be expected when the observed and predicted values are the same.

TABLE 6. Analyses of variance of size of 1-week-old wild rice seedlings among and within three populations differing in mean seed size

Variable and source of variation	MS	% variance explained	Cochran's C
Seed weight			
Among groups	5936.6***	48.8	0.475
Within groups	295.9		
Fresh weight			
Among groups	5921.1***	41.8	0.804***
Within groups	394.8		
Leaf width			
Among groups	0.121***	40.3	0.711***
Within groups	0.008		
Root number			
Among groups	14.32***	34.1	0.364
Within groups	1.26		
Dry weight			
Among groups	55.15***	32.6	0.713***
Within groups	5.16		
Leaf number			
Among groups	5.07***	31.1	0.435
Within groups	0.51		

NOTE: For each variable, the degrees of freedom for the among-population and within-population components were 2 and 57, respectively. ***, $p < 0.001$.

weight is strongly related to endosperm weight and less strongly to hull weight, and that these variables reflect a different dimension of the data than does embryo weight. This

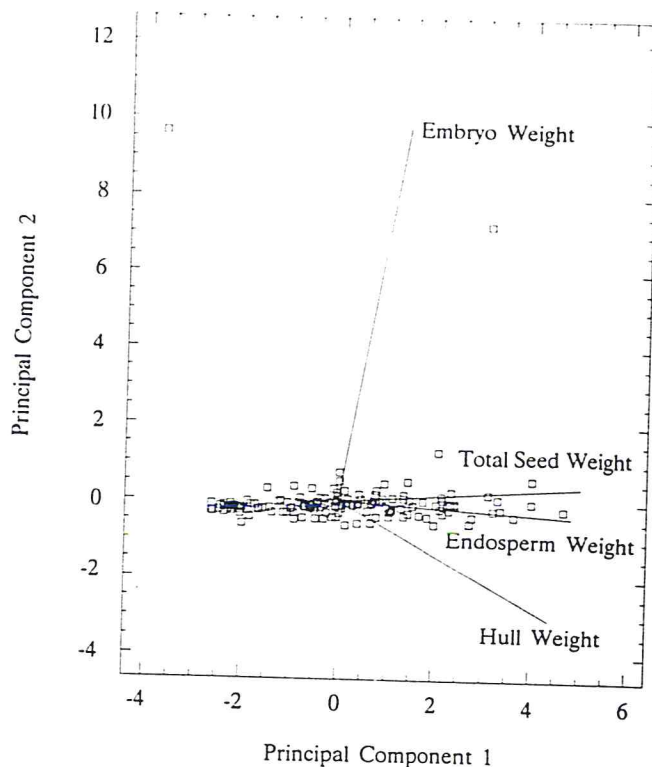


FIG. 3. Scores on first two principal components (PCs) of total and partitioned seed weight for 120 seeds from four wild rice populations differing in mean seed size. Lines are vectors expressing the relative weights of original variables in construction of the PCs.

suggests that increases in total caryopsis weight occur primarily by greater allocation to endosperm and hull tissue rather than to embryos.

Effects on germination

Incubation temperature had a dramatic effect on germination dynamics for all seed size-classes. The ANCOVA using both temperature and size class as factors showed that although both main effects were significant (Table 5), the temperature effect was much greater ($F_{1,183} = 484.3$ vs. $F_{3,183} = 3.2$). Both the population \times temperature ($F_{3,183} = 3.4$) and population \times temperature \times days ($F_{3,183} = 3.2$) interactions were also significant, indicating that both slopes and intercepts of the regression lines were sensitive to the combination of temperature and population considered. A log-log plot of proportional germination versus days with the fitted regression lines is shown in Fig. 4 for the two temperature regimes.

For all populations, initiation of germination in the first 24 h of incubation was more rapid at the higher temperature, as shown by the differences in intercepts for the two regimes. However, subsequent to the first 24 h germination rates were not significantly different in the two regimes for any of the populations. Virtually 100% proportional germination was reached in all populations after about 9 days at the high temperature, whereas the plateau was not yet reached after 14 days at the low temperature.

Germination dynamics were very similar for populations 1, 3, and 4. Population 2, of an intermediate size class, had a unique germination pattern: initial (24 h) germination was significantly higher, and the subsequent rate significantly slower,

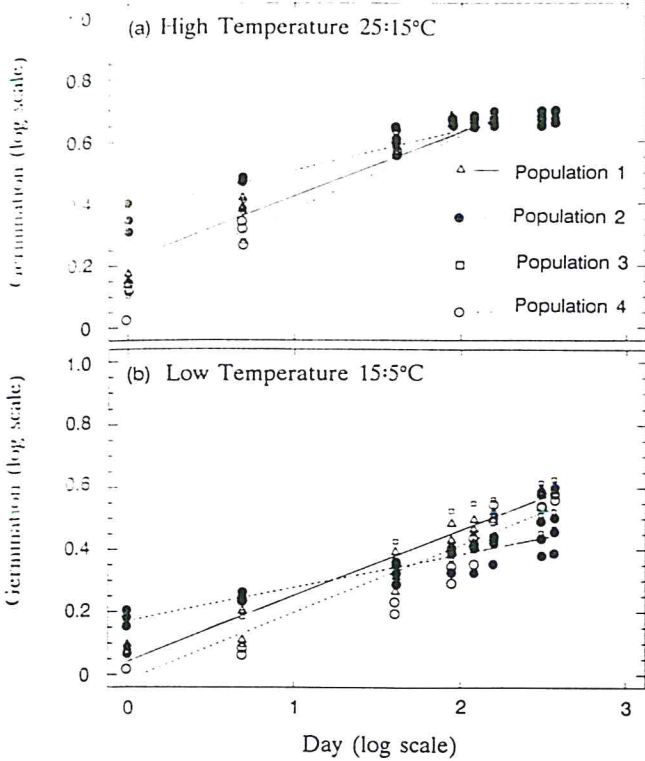


FIG. 4. Germination dynamics for seed from four wild rice populations differing in mean seed size subjected to (a) high-temperature (25:15°C), or (b) low-temperature (15:5°C) regimes. The regression lines fitted by analyses of covariance are as follows: population 1 (Whitefish Lake): (a) $y = 0.218 + 0.206x$, (b) $y = 0.041 + 0.211x$; population 2 (Red Lake): (a) $y = 0.379 + 0.128x$, (b) $y = 0.171 - 0.107x$; population 3 (Sikachu Lake) (a) $y = 0.178 + 0.225x$, (b) $y = 0.054 + 0.193x$; population 4 (Rice Lake): (a) $y = 0.144 - 0.237x$, (b) $y = -0.018 + 0.216x$. Standard errors for the intercept terms are 0.019 and 0.020 for the high- and low-temperature regimes, respectively. Standard error for the slope is 0.012 for both temperature regimes.

than for any of the others (Fig. 4). Germination in this population was also most sensitive to temperature regime.

A two-way ANOVA of total germination indicated that both temperature and population main effects and their interaction significantly ($p \leq 0.05$) affected the proportion of seeds that broke dormancy during the course of the experiment. There was a trend of decreasing total germination with increasing seed size class; for population 4 (large size class) only about 50% of the viable seeds germinated, whereas nearly 100% of population 1 seeds broke dormancy during the course of the experiment (Fig. 5). All populations had slightly lower total germination (i.e., fewer-seeds breaking dormancy) when incubated at high temperatures; this effect was most pronounced in population 2, which also had the most temperature-sensitive germination dynamics.

Seedling size

There were significant ($p \leq 0.05$) differences among the three populations for 1-week-old seedling size, with the among-population component accounting for 30–50% of total variance (Table 6). Means and standard errors for each population are shown in Fig. 6. There was a direct correspondence between initial seed size class of the population and residual seed size. For all other variables population 3

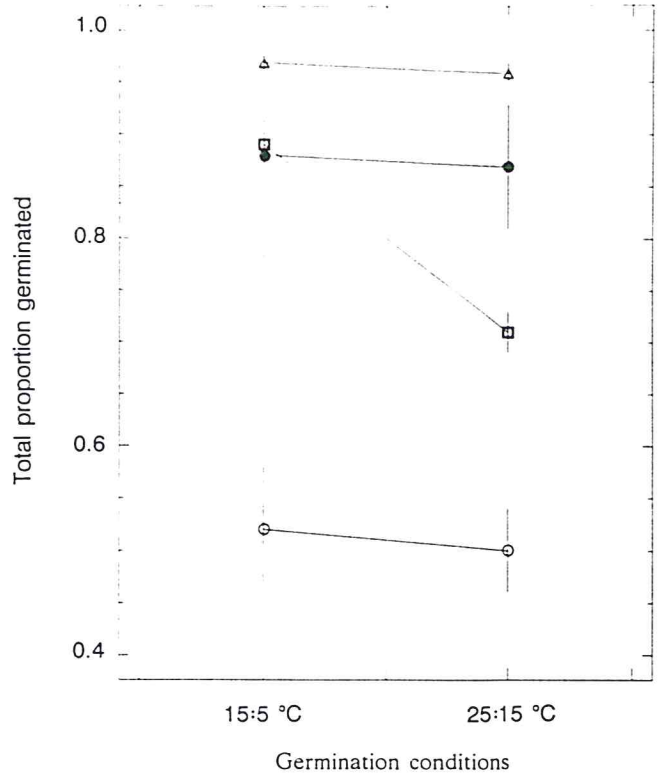


FIG. 5. Mean (± 1 SD) total proportional germination of seed from four wild rice populations differing in mean seed size subjected to a high- or low-temperature regime. Δ , population 1 (Whitefish Lake); \bullet , population 2 (Red Lake); \square , population 3 (Sikachu Lake); \circ , population 4 (Rice Lake).

(large seed size class) seedlings were significantly larger than population 1 or 2 (small and medium size class) seedlings; they had more roots and leaves, broader leaves, and higher fresh and dry weights. Population 3 seedlings were also more variable than others for fresh weight, dry weight, and leaf width, the Cochran's C-statistics indicate that the heteroscedasticity was significant. Population 1 and 2 seedlings were not significantly different from one another for root number, leaf width, or dry weight, but both leaf numbers and seedling fresh weights were higher in population 2 than in population 1 seedlings.

Discussion

This initial survey of wild rice seed size indicated that there is a greater than sevenfold variability in caryopsis fresh weight overall and that much of this variability occurs among individuals within populations. If seed size influences seedling establishment and ultimately plant success, relative seed size may be an important component of maternal plant fitness.

These studies compared populations differing in mean seed size rather than seed size classes within populations. However, because there is broad variability in seed size within each population (Fig. 1), random samples of seeds from populations differing in mean seed size will include individuals in a range likely to be encountered within a single population.

There is evidence that populations differing in mean seed size also differ in seed germinability and early seedling growth, but not germination rate. Although there were differences among the four populations for germination rates under the two temperature regimes, the pattern was not correlated with seed

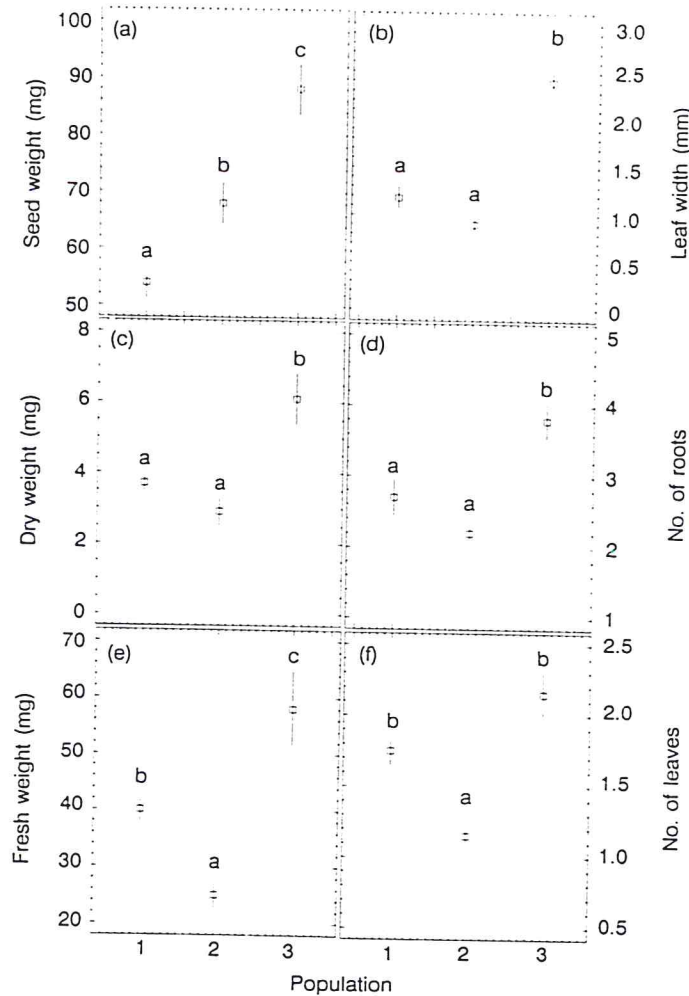


FIG. 6. Mean (± 1 SE) size of 1-week-old seedlings produced by seed from three wild rice populations with mean seed sizes of (1) 62.2, (2) 69.8, and (3) 93.7 mg. Bars identified with different letters represent significantly different mean values. (a) Residual seed weight (remaining after excision of seedling). (b) Leaf width. (c) Dry weight. (d) Root number. (e) Fresh weight. (f) Leaf number.

size class. One of the intermediate populations (population 2) differed dramatically from the other three in its germination behaviour, with a higher initial burst of germination followed by slower subsequent recruitment of new seedlings from the pool of germinable seeds. This population was also the most sensitive to variation in temperature regime (Fig. 4). Since comparisons are among populations rather than among size classes within populations, among-population genetic differences as well as differences in the environments experienced by maternal plants during seed maturation may contribute to observed patterns. Local populations of *Avena fatua* (Naylor and Jana 1976) have been found to differ in germination behaviour, and differences in temperature-sensitivity of germination have been observed among genetic strains of *Oryza* (Takahashi 1984). Geographic differences, presumably reflecting genetic differences in both germination rate and the temperature range permitting germination, have also been reported for *Betula papyrifera* (Bevington 1986). Guterman (1973, 1981) has documented numerous effects of the maternal plant environment on germination behaviour of seeds of diverse desert annuals. The interaction of genetic and environmental factors influencing germination of wild rice are poorly under-

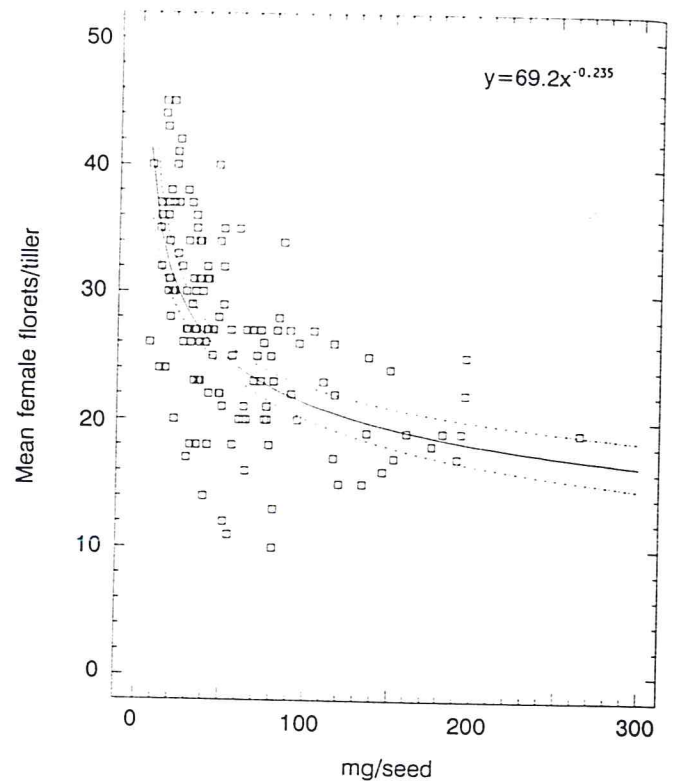


FIG. 7. Regression of mean dry weight of 10 or 20 dehulled wild rice seeds on mean number of female florets per tiller for 133 greenhouse-grown plants from eight populations. The broken lines show the 95% confidence interval for the regression line.

stood; most studies have concentrated on dormancy mechanisms rather than on the dynamics of germination per se, and none has systematically considered differences among populations in germination behaviour.

There was an apparent relationship between mean population seed size and total percent germination of viable seeds. As mean size increased, an increasing proportion of seeds remained dormant, failing to germinate during the course of the experiment. The higher incubation temperature suppressed germination of viable seeds, particularly in population 2. Increased light inhibition of germination at higher temperatures has also been reported for *A. fatua* (Sawhney et al. 1986). The influence of seed size on germination is extremely variable in different systems; there may be no discernible effect on either germination rate or percentage, an effect on one parameter but not the other, or an effect of seed size on both rate and percent germination. In some cases, the effects vary depending on the germination conditions considered, on the life history or degree of inbreeding of the population considered, and (or) on the position of the seed on the maternal plant. In most species for which a seed-size effect has been observed, percent germination or percent emergence increases with increasing seed size (e.g., Stanton 1984 with *Raphanus raphanistrum*; Winn 1985 with *Prunella vulgaris*; Hendrix 1984 with *Pastinaca sativa*; Schaal 1984 with *Lupinus texensis*). Few of these studies determined whether seeds that fail to germinate or emerge do so because they are inviable or as a consequence of prolonged dormancy.

The mechanism by which dormancy is maintained in *Z. palustris* remains uncertain. Mechanical impedance of the pericarp to embryo emergence may play a role (Simpson 1966),

... in the later stages of dormancy (Cardwell et al. 1978). There is also evidence that germination inhibitors are present in the hull and pericarp of fresh seed, and it has been suggested that the initial period of after-ripening is required for their removal by metabolism or leaching (Cardwell et al. 1978). Albrecht et al. (1979) have suggested that abscisic acid, especially in the pericarp and embryo, may be involved in the induction of germination in dormant grain. It is possible that large seeds have thicker pericarps that offer more mechanical resistance to germination, and (or) higher concentrations of germination inhibitors relative to embryo size, leading to higher proportions of seeds that exhibit prolonged dormancy. Conversely, some other mechanism entirely may be involved in the induction and maintenance of secondary dormancy.

This study indicated a significant positive relationship between mean seed size and mean seedling size in *Z. palustris*. Similar results have been observed for many species (for review see Roach and Wulff 1987; McGinley et al. 1987), although the effect is not universal (e.g., Carelton and Cooper 1972). Fewer studies have examined the relationship between seed size and adult plant size and fecundity, but those that have yielded mixed results. Many studies show that the apparent effect of seed size declines over time (Roach and Wulff 1987), but effects are more persistent when plants are evaluated in the field or under imposed competitive conditions (Stanton 1984; Wulff 1986b). It is likely that in many systems the ultimate effects of seed size are secondary and arise as a consequence of an initial size hierarchy established early in development (Schaal 1984). The long-term influence of seed size on adult plant size and fecundity in *Z. palustris* has yet to be determined, but these studies have demonstrated the potential for such effects either directly or via the establishment of a seedling-size hierarchy.

Although the production of seeds that give rise to large seedlings has obvious potential advantages for the parental plant, the advantages of producing a higher proportion of seeds with prolonged dormancy are not as readily apparent. Of course, it is possible that the production of seeds with lower initial germinability is not advantageous to the parent plant at all, but that prolonged dormancy simply occurs as an unavoidable physiological consequence of increased seed size that may be selected for other reasons. On the other hand, the production of seeds that will be recruited into the population over more than one season may have positive advantages.

The production of a diverse population of seeds by an individual, such that only a portion are immediately germinable, even under optimum conditions (heteroblasty), is prevalent among desert annuals. These plants occupy a habitat characterized by extreme temporal variability, and it has been suggested that plasticity of seed dormancy in response to the environment experienced by the maternal plant during seed maturation may be an adaptive "bet-hedging" strategy (Gutterman 1973, 1981). The genetic versus environmental basis of variation in seed dormancy has not been investigated in *Z. palustris*, but a similar argument may apply at the population level. Many wild rice populations are subject to fluctuating environmental conditions leading periodically to reproductive failure, either as a consequence of sudden changes in water level resulting in drowning or lodging, or as a consequence of premature curtailment of the seed maturation period by early fall frosts. The ability to spread seedling recruitment over several seasons by the production of seeds with a prolonged dormant period may confer an adaptive advantage to

parent plants in such unpredictable environments. Previous work (Counts and Lee 1987, 1990) has shown that north-western Ontario wild rice populations occurring in regions with more severe climatic conditions (fewer growing degree-days, with a greater risk of early fall frost) are characterized by small plants that mature earlier and produce fewer seeds per stem than populations subject to more moderate climates. Although no significant consistent relationship between seed size and climate was found, regression analysis of data obtained for greenhouse-grown plants from eight populations (see Counts and Lee 1987 for the experimental protocol) shows that there is a significant ($R^2 = 0.348$; $df = 132$; $p < 0.001$) negative exponential relationship between seed number and seed size (Fig. 7). Thus, as is commonly found, plants that produce fewer seeds tend also to produce larger seeds. Plants occurring in severe climates on the average produce fewer seeds, and therefore they may also be expected to produce a higher proportion of large seeds that have a greater tendency to delay germination and remain dormant in the seed bank. Critical work to test a possible relationship between environmental unpredictability in general and seed size and (or) prevalence of prolonged dormancy at the population level has not yet been carried out. Future studies should also consider effects of seed size on germination and seedling growth within populations and on the relationship between seedling size and adult plant size and fecundity.

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