Plant Breeding **132**, 620–624 (2013)
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doi:10.1111/pbr.12106

Selection by seed weight improves traits related to seedling establishment in *Panicum coloratum* L. var. *makarikariense*

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With 2 figures and 2 tables

Received December 14, 2012/Accepted July 29, 2013
Communicated by M. Prasad

Abstract

Selection for heavy seed was implemented to overcome establishment problems in *Panicum coloratum* var. *makarikariense*. A collection covering the genetic diversity of the species available in Argentina was used as a base population (BP), and two cycles of recurrent phenotypic selection to increase seed weight were performed. Seedlings, obtained from seeds from each cycle and the BP, were further evaluated in the greenhouse. An increase of 17% in mean seed weight was obtained after two cycles of recurrent selection. No differences in germination or emergence were detected among the selected materials and the BP. However, seedlings from selected materials were taller and showed higher leaf elongation rate, adventitious roots elongation rate and total growth rate than that from BP. This research also revealed that in *P. coloratum* var. *makarikariense*, more vigorous seedlings can be selected from genotypes that produce heavier seeds.

Key words: recurrent selection — seed weight — seedling establishment — panicum — plant breeding — C4 grasses

The continuous increase in the area dedicated to agriculture that has taken place in Argentina in the last decade (Manuel-Navarrete et al. 2009) has displaced livestock production to areas with adverse environmental conditions (e.g. saline soils, high temperatures, high radiation, low air humidity, flooding) in which C4 species usually perform better than their C3 counterparts (Sage 2004, Rearte 2007). Thus, a continuous effort to develop species better adapted to those areas has been reported (Taleisnik et al. 1998, Ribotta et al. 2005, Griffa et al. 2010, Privitello et al. 2010).

Panicum coloratum is an open-pollinated, warm-season perennial grass native to Africa that has been extensively used in pastures and revegetation projects in the USA, Australia and South America (Bovey et al. 1986). According to Tischler and Ocumpaugh (2004), this species consists of two botanical varieties, *P. coloratum* var. *coloratum* and *P. coloratum* var. *makarikariense*. In particular, *P. coloratum* var. *makarikariense* is well adapted to heavy soils and is able to tolerate periods of drought followed by seasonal flooding (Tischler and Ocumpaugh 2004). In addition, the species is highly productive and has an above-average forage quality for a warm-season grass (Stritzler et al. 1996).

Difficulties in stand establishment have been recognized as a common problem in species producing small seeds (Green and Hansen 1969, Carleton and Cooper 1972). As several C4 grasses (Moser 2000), *P. coloratum* seems not an exception. In fact, this species frequently shows failures in pasture establishment generally assumed to be related to low seedling growth and to excessive mesocotyl elongation (Lloyd 1981, Tischler and Voigt 1987).

Therefore, a rapid growth and development of leaves and adventitious roots are necessary for successful seedling establishment, allowing a greater acquisition of resources (Moser 2000). These, in turn, improve both competitiveness and seedling capacity to surmount adverse situations (Essau 1960, Hyder et al. 1971). In this sense, several traits associated with improved seedling growth were positively correlated with heavy seed (Trupp and Carlson 1971, Ludlow and Wilson 1972, Silcock 1980, Tischler et al. 1989, Alizaga et al. 1994, Smart and Moser 1999, Waldron et al. 2006).

Because seed size is a quantitative character (governed by several genes), one way to indirectly improve seedling vigour is to increase seed weight through selection. Breeding programmes selecting for seed weight showed concomitantly changes in germination, emergence, number and length of adventitious roots and seedling biomass (Trupp and Carlson 1971, Wright 1977, Hussey and Holt 1986, Boe and Johnson 1987).

Based on the successful experience with *P. coloratum* cv. 'Verde' (Holt et al. 1983) and in a significant (and positive) genetic correlation between seedling weight and seed weight observed in *P. coloratum* var. *makarikariense* (Dreher 2011), a breeding programme to increase the seed weight in *P. coloratum* var. *makarikariense* was developed. This study reports the effect of recurrent selection to modify seed weight and consequences on both the germination/emergence processes and the seedling performance, in the selected populations. The hypotheses were that (i) seed weight in *P. coloratum* var. *makarikariense* is able to be increased by recurrent selection, (ii) germination and emergence percentages are increased by increments in seed weight and (iii) seedling vigour related attributes increase in response to seed weight increments.

Materials and Methods

Site and climate: A breeding scheme of recurrent phenotypic selection with restricted intercrossing was carried out at the National Institute of Agricultural Technology (INTA) EEA near Rafaela, Argentina (31°11′S, 61°29′W) on a Typic Argiudoll soil (MO: 3.3 g/kg; P Bray I: 45 ppm; pH: 7.1). Accumulated precipitations for the period of study (January to May) were superior (870 mm), similar (501 mm) and inferior (404 mm) than historical values in 2007, 2008 and 2009, respectively. In turn, mean daily temperature (T, °C) and incident photosynthetic active radiation (PAR Mj/m^2.day) were quite similar (2007: 20.4°C, 8 Mj/m^2.day; 2008: 21.1°C, 9 Mj/m^2.day; 2009: 22.1°C, 9 Mj/m^2.day) than historical records (21°C, 9 Mj/m^2.day).

Selection cycles: Two cycles of divergent selection for seed weight were conducted. The base population (BP) consisted of 84 individuals selected from a germplasm source established in a spaced-plant nursery from ramets collected out of pastures under different management regimes. To initiate selection, the seed weight of all plants within the BP was determined. In 2007, seeds were harvested manually from individual plants and collected in a paper bag. In the laboratory, seeds were manually threshed and blown to remove glumes and other residuals. Seeds were classified as mature when they presented a brown dark colour. Immature seeds were disregarded. Seed weight per plant was obtained by averaging the weight of three groups of 100 seeds each.

The extreme 14% of the plants producing the heaviest seed were selected at each selection cycle. This selection intensity (i = 1.59, Brown and Caligari 2009) was less severe than the ones used in reported selection schemes in other forage grasses (Wright 1976, Hussey and Holt 1986) to avoid possible endogamy effects due our rather small-numbered BP.

Seeds were pregerminated in Petri dishes and planted in 300 cm^3 pots in groups of three and kept in the greenhouse. When the plants reached a 3–5 tiller stage, they were transplanted in an isolated (at least 300 m distance from each other) polycross spaced-plant field nurseries to avoid intercrossing.

The heavy seed first cycle (HS1) crossing block contained 240 plants that were arranged in five blocks. The heavy seed second cycle (HS2) crossing block was composed by 160 plants arranged in five blocks. In all crossing blocks, distance between blocks was 120 cm, and within each block, plants were planted in groups of four with the same origin (half-siblings) at a 0.6 m distance between them. Immediately after transplanting, plants were watered once and fertilized with nitrogen (15 g/m^2). Seeds from crossing blocks were collected in late autumn with the aid of a seed-collecting tramp (Young 1986). Each year, seeds were collected from all available populations, to counteract for environmental differences. Seeds were transferred to the laboratory, processed and weighted as described previously.

Experiment 1 – Germination percentage: Seeds and seedlings performance derived from the BP, heavy seed first cycle (HS1) and heavy seed second cycle (HS2) were evaluated. This experiment was carried out under greenhouse conditions (T = 27°C; PAR = 6 Mj/m^2.day) from 11 January to 19 January, 2011, with seeds collected in 2009.

To evaluate the germination percentage (GP), 100 seeds from each population were randomly selected, divided in groups of 20 seeds and placed in Petri dishes with distilled water. The number of germinated seed per dish was counted up at 2, 4, 6 and 8 days after trial set-up.

Experiment 2 – Emergence percentage and seedling vigour: This experiment was carried out in the same greenhouse from 11 January to 8 February, 2011; conditions were quite similar than those previously described (T; PAR). Seeds from BP, HS1 and HS2 were sown in rows 5 cm apart in expanded polystyrene trays of 24 cm width, 38 cm length and 10 cm depth filled with the upper 20 cm of the Typic Argiudoll soil mentioned above. Eighteen seeds of each population were arranged at 2 cm distance between them and at a depth of 0.5 cm in rows distributed at random in five trays, in a complete random design. Trays were watered with tap water by capillarity on first week and by sprinkling until the end of the trial.

Date of emergence of each seedling was registered daily. Percentage of emerged seedlings (plumule emerged above the soil surface) and tiller height (distance from the soil until the top of the extended tiller) were registered at 7, 15, 21 and 28 days after sowing. At 28 days after sowing, five seedlings from each population on each tray were removed from the soil and gently washed. Total blade length, the number of leaves, total length of adventitious roots, the number of adventitious roots and seedling dry weight of complete seedling were measured.

Leaf appearance rate (leaves/day.seedling), leaf elongation rate (cm/day.seedling), total growth rate (g/day.seedling), adventitious roots appearance rate (roots/day.seeedling) and adventitious roots elongation rate (roots/day.seedling) were calculated for each plant, as the quotient between data at 28 days after sowing and days lapsed from emergence till harvest at 28 days after sowing.

Statistics: Within each year, mean seed weight of populations was analysed by ANOVA, followed by orthogonal contrast. Contrasts were made to compare HS2 with the rest of populations and HS1 with BP. Seed weight from BP was compared between years by orthogonal contrasts (2007 vs. 2008; 2009 vs. 2008 and 2007). Selection response (R) was estimated as the difference between the mean of the progeny and the mean of the parental population from the same year. Selection differential (S) was calculated as the difference between the mean of the selected population and the mean of the parental population (Brown and Caligari 2009). Realized heritability estimates were obtained as h^2 = R/S (Falconer 1986).

Two-factor analysis of variance with repeated measures at 0.05 level was performed for germination percentage, emergence percentage and height. Covariance structure was heterogeneous autoregressive of order 1. Least significance difference was applied when ANOVA was significant.

Analysis of variance (P = 0.05) followed by orthogonal contrasts, as that mentioned above for populations comparison, was applied for leaf appearance rate, total growth rate, adventitious roots appearance rate and adventitious roots elongation rate. Total growth rate was transformed by square root to account for variant heteroscedasticity. Leaf appearance rate data were not normal, and transformation did not help to improve normality, so Kruskal–Wallis test was applied (P = 0.05).

Analysis of variance (P = 0.05) followed by orthogonal contrasts, as that mentioned above for populations comparison, was applied too for seedling characters measured on day 28 after sowing. Transformations were applied as necessary.

Results

Selection cycles

Two cycles of selection increased the mean seed weight by 17%, obtaining approximately 12% of the increment in the first cycle and 5% in the second cycle (Table 1). Interestingly, mean seed weight produced in 2009 by the BP was different from those produced in 2008 and 2007 years (P < 0.05). This could be related to a reduction in precipitation along the successive growing seasons.

Regarding the selection cycles, seed weight of the BP in 2007 was 1.22 ± 0.12 mg per seed, and mean seed weight of the plants selected to start the first cycle was 1.40 ± 0.43 mg per seed (Table 1).

Mean seed weight for HS1 was different from BP (P < 0.05) in 2008. For this cycle, selection response, selection differential and realized heritability for HS1 were 0.13, 0.18 and 0.72 mg, respectively. Mean seed weight of the plants selected to start the second cycle was 1.49 ± 0.53 mg per seed.

Table 1: Weight per seed of base and response populations, in the years of study

Population	2007	2008	2009
BP	1.22 ± 0.12	1.21 ± 0.09	1.17 ± 0.08
HS1		1.34 ± 0.12	1.31 ± 0.11
HS2			1.37 ± 0.09

Values are given as phenotypic means ± standard deviation (mg).
BP, base population; HS1, first cycle for heavy seed; HS2, second cycle for heavy seed.
Contrasts evaluated were 'HS1 vs. BP' (P < 0.05) and 'HS2 vs. rest of populations' (P < 0.05) in 2008 and 2009, respectively. In turn, seed weight differences between years were evaluated for BP by the following contrasts: '2007 vs. 2008' (P > 0.05) and '2009 vs. rest of years' (P < 0.05).

In 2009, mean seed weight of the HS2 was 1.37 ± 0.09 mg per seed, significantly superior to BP and HS1 ($P < 0.05$). Selection response, selection differential and realized heritability for this cycle were 0.06, 0.15 and 0.4 mg, respectively. Realized heritability diminished as selection for heavy seed cycles progress.

Material evaluation

Populations did not differ from one another for germination percentage (date by population interaction was not significant; Fig 1a). A significant date by population interaction was observed for emergence percentage. However, no differences between populations in emergence percentage were detected at any of the sample dates (Fig. 1b). Remarkably, in all evaluated populations, final values of germination percentage (~90%) were 25% higher than the final values of emergence percentage (~65%).

Date by population interaction was significant for tiller height. Tiller height was similar among populations until 15 days after sowing. HS2 tillers were significantly taller than those from the other two populations at 21 days after sowing, while all three populations differed at the last sampling date, being HS2 superior, HS1 intermediate and BP inferior (Fig. 1c).

Leaf elongation rate, adventitious root elongation rate and total growth rate were higher in HS2 than the remainder of the populations (Table 2). Therefore, the population with higher seed weight (HS2) showed concomitant superior values ($P < 0.05$) of seedling traits than the rest of populations at the end of the trial, as shown in Fig. 2. No significant differences were detected between populations for leaf appearance rate and adventitious roots appearance rate (Table 2).

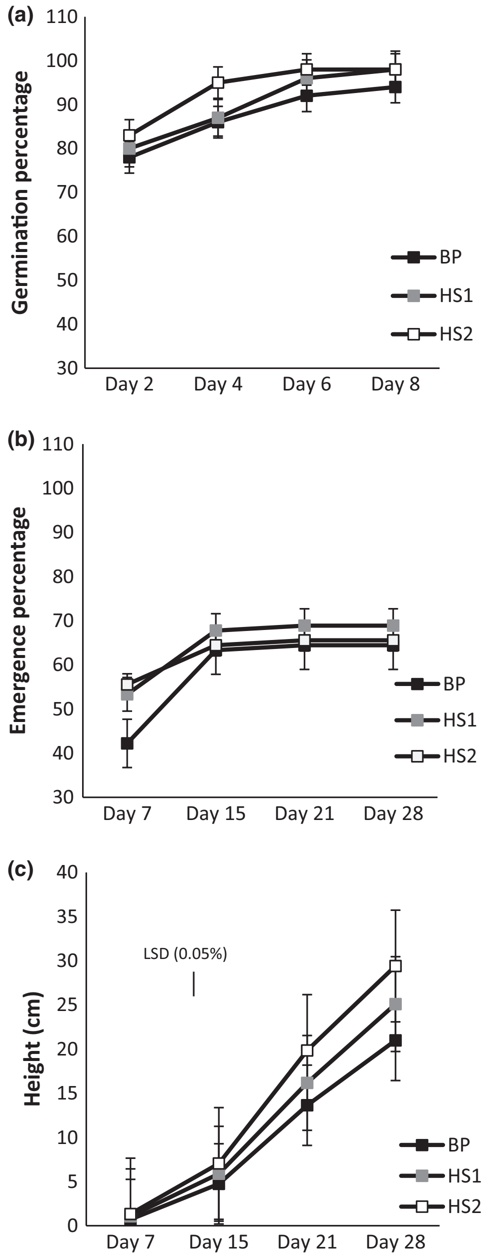

Fig. 1: Germination percentage (a), emergence percentage (b) and height (c) in seedlings of base population (BP), first (HS1) and second (HS2) cycles for heavy seed of *Panicum coloratum* var. *makarikariense*. Population-by-date interactions were significant ($P < 0.05$), except for (a). Bars indicate mean standard error. LSD: least significant difference

Discussion

Effect of selection on seed weight

Results from this study demonstrate that recurrent phenotypic selection is effective in changing the mean seed weight in *P. coloratum* var. *makarikariense*. In such sense, estimates of realized heritability to increase seed weight of the present study are in agreement with narrow-sense heritability estimates of seed weight reported elsewhere (Potts and Holt 1967, Wright 1976).

The fact that seed weight is modified by a few cycles of selection supports the hypothesis that the character is highly heritable, and that most of the observed phenotypic variation is additive. As it was previously pointed out, seed weight is likely a quantitative trait and shifts in population means through selection pressure may or may not occur rapidly (Wright 1976). In addition, the fact that changes in seed weight in this study are lower than those obtained in other studies (Wright 1976, Hussey and Holt 1986) suggests that further improvements in seed weight may be obtained if higher selection pressures are applied. In this study, selection responses after each cycle are quite different although similar selection intensities were applied in the two cycles. Variation in the pattern of response was also reported in other grass species (Hussey and Holt 1986). In general, a decrease in phenotypic response and a reduction in the estimation of realized heritability are expected as selection cycles progress (Falconer 1986). The fact that standard deviation values for successive cycles are similar suggests that variation in the population still remains and progress might be expected if other cycles of selection are performed.

Effect of seed weight on germination

In this study, differences in mean seed weight are related neither to differences in emergence percentage nor to germination percentage. These findings are unexpected given results reported elsewhere (Trupp and Carlson 1971, Stanton 1984, Carren et al. 1987, Aiken and Springer 1995). However, Tomás et al. (2007) found that seed weight was highly correlated to germination percentage up to 1.34 mg per seed; beyond that point, germination percentage stabilized at 84%, and further increases in seed weight did not increase germination rate. We infer that no changes in germination percentage among populations are observed because populations' seed weight at the present study was close to the above-mentioned threshold point (1.17–1.37 mg per seed).

Table 2: Seedling characteristics observed in populations of *Panicum coloratum* var. *makarikariense* at 28 days after sowing

Population	LAR (leaves/day)	LER (cm/day)	ARER (cm/day)	ARAR (roots/day)	TGR (mg/day)
BP	0.24 ± 0.01	2.1 ± 0.18	0.92 ± 0.10	0.2 ± 0.01	4.2 ± 0.57
HS1	0.24 ± 0.005	2.5 ± 0.17	0.96 ± 0.08	0.2 ± 0.01	5.3 ± 0.56
HS2	0.25 ± 0.01	2.8 ± 0.18	1.28 ± 0.11	0.2 ± 0.01	6.4 ± 0.66
P-value	0.247	0.021	0.018	0.131	0.015

Values are given as means (n = 25) and standard error per seedling.
BP, base population; HS1, first cycle for heavy seed; HS2, second cycle for heavy seed. LAR, leaf appearance rate; LER, leaf elongation rate; ARER, adventitious roots elongation rate; ARAR, adventitious roots appearance rate; and TGR, total growth rate.
Contrasts evaluated were 'HS1 vs. BP' ($P > 0.05$) and 'HS2 vs. rest of populations' ($P < 0.05$).

Interestingly, seedling emergence percentage for the present study is close to those previously reported (Lodge and Harden 2009). Nonetheless, differences between germination percentage (~90%) and emergence percentage (~65%) should be taken into account before recommending an appropriate seed sowing rate, because almost 25% of the seedlings would be expected not to survive. Further research is needed to elucidate the reason for this reduction or the loss of seedlings. This would provide better insight for recommending the appropriate seeding rate for *P. coloratum* var. *makarikariense.*

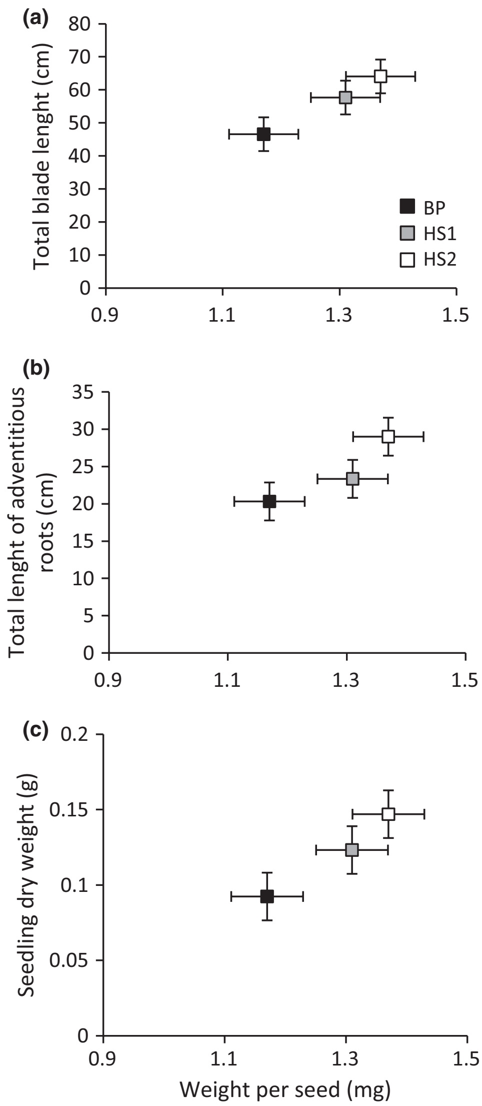

Fig. 2: Seed weight per seed and its corresponding seedling values at 28 days after sowing in base population (BP), first (HS1) and second (HS2) cycles for heavy seed. Bars indicate mean standard error. In all cases, contrasts evaluated were 'HS1 vs. BP' ($P > 0.05$) and 'HS2 vs. rest of populations' ($P < 0.05$)

Effect of seed weight on seedling vigour

Selection to increase seed weight is also an effective method to increase seedling vigour in *P. coloratum* var. *makarikariense*. Similar results were previously reported for other species (Trupp and Carlson 1971, Wright 1976, 1977). It is well known that the probability of a successful seedling establishment and a better competitive ability to access to light and nutrients is higher in individuals deriving from heavier seeds (Westoby et al. 2002). Evidence supporting the relationship of larger seed weight and thus larger food reserve with an extended prephotosynthetic growth, greater embryo size and eventually more vigorous seedling is well documented (Bretagnolle et al. 1995, Moser 2000, Westoby et al. 2002).

The fact that selection did not change rates of developmental processes (i.e. leaf and adventitious root appearance rates) suggests that improvement in seedling vigour is only related to growth processes (i.e. leaf and adventitious root elongation rates). These findings indicate that contrary to germination/emergence processes, seedling vigour could be further improved by selecting plants with heavy seeds. A better ability to capture and use resources (e.g. light, water, nutrients) at the seedling stage is not minor because *P. coloratum* var. *makarikariense* had stand failures in early stages of pasture establishment (Lodge et al. 2009, 2010, Boschma et al. 2010).

Conclusions

This study demonstrates that seedling vigour was improved by indirect selection to increase seed weight. However, further improvements in germination and emergence processes by increments in seed weight are not feasible.

In addition, the striking reduction observed between germination and emergence percentages points out the need for additional research to overcome this problem.

Acknowledgements

The research programme was founded by the Instituto Nacional de Tecnología Agropecuaria (INTA), proyecto específico AEFP 261821. Mabel Giordano was supported partially by an undergraduate fellowship awarded by Asociación Biológica de Santa Fe (Bios). We are grateful to Byron Burson for his helpful revision of an earlier version of the manuscript. We are also grateful to comments of an anonymous reviewer, which improved our manuscript.

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