

Selection of full-sib families of *Panicum maximum* Jacq under low light conditions¹

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ABSTRACT

The silvopastoral system is a viable technological alternative to extensive cattle grazing, however, for it to be successful, forage grass genotypes adapted to reduced light need to be identified. The objective of this study was to select progenies of *Panicum maximum* tolerant to low light conditions for use in breeding programs and to study the genetic control and performance of some traits associated with shade tolerance. Six full-sib progenies were evaluated in full sun, 50% and 70% of light reduction in pots and subjected to cuttings. Progeny genotypic values (GV) increased with light reduction in relation to plant height (H) and specific leaf area (SLA). The traits total dry mass accumulation (DM) and leaf dry mass accumulation (LDM) had GV higher in 50% shade and intermediate in 70% shade. The GV of tiller number (TIL) and root dry mass accumulation (RDM) decreased with light reduction. The highest positive correlations were obtained for the traits H and RDM with SLA and DM; the highest negative correlations were between TIL and SLA and RDM, and H and LDM. The progenies showed higher tolerance to 50% light reduction and, among them, two stood out and will be used in breeding programs. It was also found that it is not necessary to evaluate some traits under all light conditions. All traits had high broad sense heritability and high genotypic correlation between progenies in all light intensities. There is genetic difference among the progenies regarding the response to different light intensities, which will allow selection for shade tolerance.

Key words: biomass accumulation, hybrids, morphophysiology, shading.

RESUMO

Seleção de progênes de irmãos completos de *Panicum maximum* Jacq sob condições de redução de luminosidade

A implantação de sistemas silvipastoris é uma alternativa tecnológica à criação extensiva de gado e, para que haja sucesso, é necessário identificar genótipos de gramíneas forrageiras adaptados à redução de luminosidade. O objetivo deste estudo foi selecionar progênes de *P. maximum*, tolerantes à redução de luminosidade, para uso em programas de melhoramento, e estudar o controle genético e o desempenho de alguns caracteres associados à tolerância. Foram avaliadas seis progênes de irmãos completos, a sol pleno, a 50% e a 70% de redução da luminosidade, em vasos e sob cortes. Os valores genotípicos (VG) das progênes, em relação à altura das plantas (ALT) e à área foliar específica (AFE), aumentaram com a redução da luminosidade. Para os caracteres acúmulo de massa seca total (MS) e massa verde de lâminas foliares (MSVLF), esses VG foram maiores, com 50%, e interme-

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diários, com 70% de redução da luminosidade. Para o número de perfilhos (PERF) e para o acúmulo de massa seca de raízes (MSR), os VG das progênies diminuíram com a redução de luminosidade. As correlações mais altas e positivas foram obtidas para os caracteres ALT e MSR com AFE e MS; as mais altas e negativas foram entre PERF com AFE e MSR, e ALT com MSVLF. As progênies avaliadas apresentaram maior tolerância a 50% de redução de luminosidade, das quais duas destacaram-se e deverão ser usadas no melhoramento. Evidenciou-se, também, que não é necessária a avaliação de algumas características em todos os níveis de luminosidade. Todos os caracteres apresentaram alta herdabilidade no sentido amplo e alta correlação genotípica entre as progênies, ao longo dos níveis de luminosidade. Há uma diferença genética entre as progênies, quanto à resposta aos diversos níveis de luminosidade, o que permitirá a seleção para a tolerância ao sombreamento.

Palavras-chave: acúmulo de biomassa, híbridos, morfofisiologia, sombreamento.

INTRODUCTION

The use of *Panicum maximum* cultivars for pasture establishment in conventional production systems has grown in Brazil, and there is an increased demand of genotypes for silvopastoral areas. The development of new cultivars of this species for silvopastoral systems is possible, since these plants have satisfactory tolerance to light reduction (Wong & Wilson, 1980; Eriksen & Witney, 1981; Andrade *et al.*, 2004).

Panicum maximum has a high genetic variability in its center of origin and Brazil has a large germplasm bank (Embrapa Beef Cattle), allowing the improvement of the species. Of the 426 accessions in the germplasm bank (Jank *et al.*, 1997), 21 were evaluated for tolerance to shading in a previous study (Jank *et al.*, 2005; 2006). A high variability was found in response to shading and nine accessions were identified as promising. Individuals adapted to light reduction must have biomass accumulation similar to that obtained in full sun and keep qualitative forage characteristics. Forage biomass accumulation results from genetic and environmental factors, which enable the selection of genotypes better fit for specific environments through quantitative morphological and physiological characteristics.

Therefore, the objective of this study was to select progenies of *P. maximum* tolerant to light reduction for breeding programs and study the genetic control and performance of some traits associated with this tolerance.

MATERIAL AND METHODS

The experiment was conducted at Embrapa Beef Cattle, Campo Grande, MS, located at 20° 27' S and 54° 43' W, from November 2004 to October 2005. The study area has a tropical rainy savanna climate, subtype Aw.

Six *P. maximum* progenies were evaluated in three light intensities. The progenies derived from controlled

crosses between six apomictic parents and two sexual parents, all tetraploid. The crosses designating the full sib progenies are: (i) progeny 1: S10 (sexual) x cv. Mombasa (apomictic); (ii) 2: S12 (sexual) x PM23 (apomictic); (iii) 3: S12 (sexual) x cv. Tanzania-1 (apomictic); (iv) 4: S12 (sexual) x PM10 (apomictic); (v) 5: S10 (sexual) x PM13 (apomictic); and (vi) 6: S10 (sexual) x PM31 (apomictic). The progenies 1, 5 and 6 and the progenies 2, 3 and 4 are also half-sibs as they have the sexual progenitor in common.

The experiment was arranged in a split plot randomized block design with four replications. The main plots were full sun, 50% and 70% light reduction and the subplot consisted of four individuals of each progeny planted separately in pots.

The pots were filled with Chernosol Haplic soil (Embrapa, 2013), 5.81 pH; 70.7% base saturation; 10.1 base sum; 14.3 T CTC; 11.9 mg/dm³ P (Mehlich 1); 1.47 K; 5.75 Ca; and 2.9 Mg (cmol.dm⁻³). Before planting the seedlings, the soil was fertilized with 50 kg.ha⁻¹ P₂O₅ (superphosphate) and 75 kg.ha⁻¹ of potassium chloride. Individuals of each progeny were transplanted to pots in December 2004. The experiment started in February 2005, when the plants were cut to the height of 20 cm above the soil, fertilized with 10 ml per pot of a solution of 200 g of ammonium sulfate and 100 g of potassium chloride in 1 L of water, and then the pots were exposed to the different light intensities. The same fertilization was also used at the end of March 2005.

After the full establishment of forage, the plots (size 6 m x 6 m) were covered with a plastic net (50 and 70% shading) at the height of 2.0 m above the ground.

Morphophysiological evaluations were carried out for the traits plant height (H), number of tillers (TIL) and specific leaf area (SLA). Plants were measured in cm from the base of the stem to the tip of the stretched leaves. Tillers were counted per pot. SLA was estimated by measuring the leaf area of four medium leaves in each

plant using the leaf area meter Li-Cor®, then drying them in an air-forced drier at 65 °C to constant weight and weighing on a digital scale. SLA was calculated by dividing the leaf area by the dry weight of the four leaves and expressed as $\text{dm}^2 \cdot \text{g}^{-1}$.

Leaf blade dry mass accumulation (LDM, g/pot) and total dry mass accumulation (DM, g/pot) were obtained from hand separation of leaf blades, stem including leaf sheath and dead material, which were dried in an air-forced drier at 65 °C to constant weight and weighed on a digital scale.

In this work, we will not show statistical results for stems, sheaths and dead material due to their low genetic control. Root dry matter accumulation (RDM, g/pot) was evaluated at the fourth cutting. Roots were washed in running water, dried in the sun and later in an air-forced drier at 65 °C to constant weight and weighed on a digital scale. The four evaluations of individual plants from each progeny were carried out on 22/03, 26/04, 04/07 and 12/09, 2005. The traits number of tillers, height and specific leaf area used the means of four evaluations, while LDM and DM used the sum of the four evaluations.

Data were analyzed using the methodology of mixed linear models (REML/BLUP procedure), by analyzing the means of the plots of each progeny, as in Resende (2002a). Light and block were treated as fixed effects and the remaining as random effects. Significance of random effects of progenies and progeny x light interaction was determined by the likelihood ratio test based on model deviance, considering each of the effects separately, according to Resende (2007). Statistical analysis of data was performed according to the model:

$$Y_{ijk} = \mu + l_i + b_j + lb_{ij} + g_k + lg_{ik} + lb_{(ijk)}$$

where, μ is the overall mean effect; l_i is the effect of the i th light intensity; b_j is the effect of the j th block; lb_{ij} is the effect of the ij th error; g_k is the effect of the k th genotype; lg_{ik} is the effect of the interaction light x progenies and $lb_{(ijk)}$ is the error b . The following parameters were estimated: coefficient of genotypic determination (CGD) or heritability (in the broad sense of the genotypic effects of the progenies in the subplots); Broad sense heritability (adjusted) of progeny mean (h_{mg}^2); genotypic correlation between progenies for light intensities (r); coefficient of genotypic variation associated with progeny (CGV); coefficient of residual variation (CRV) and coefficient of determination of the effects of the interaction progenies x light intensities (CDI). The genotypic correlation between characters (r_{xy}) was also estimated.

The genetic evaluation for estimation of genetic parameters and prediction of genotypic values of the progenies was performed with the software SELEGEN -

REML/BLUP procedures (Resende, 2002a and b). Comparisons between light intensities (fixed) were performed using the Tukey test at 5% probability.

RESULTS AND DISCUSSION

The coefficient of genotypic determination (CGD) was moderate or high (greater than 30%) for most traits, except for RDM (Table 1). CGD explains the amount of the phenotypic variability that was due to genotype variation, i.e., it is equivalent to the broad sense heritability of the trait. Thus, in this case, it indicated that for the progenies evaluated, H and TIL were the most heritable traits and should be more easily selected and have the largest gains in breeding programs. Also, the heritability (adjusted) of progeny mean (h_{mg}^2) was high for all the traits in the three light intensities (LI) (Table 1). In this case, progeny selection is facilitated for all traits, especially considering that, in progenies from crosses between apomictic and sexual genotypes, there is 1:1 segregation for mode of reproduction (Savidan, 1980). Therefore, apomictic individuals will have the genotype fixed, containing additive and dominant effects, regardless of the genetic control of the trait.

The genotypic correlations between the progenies over the light intensities (r) were high for H, LDM and RDM (> 70%) and above 98% for TIL, SLA and DM. These high correlations provide genetic stability in the case of evaluation in other light intensities, even considering that progeny x light interactions were significant for most traits, except for DM and SLA. A similar result was reported by Jank *et al.* (2006) for 28 genotypes of *P. maximum*, with r greater than 78%, between the same light intensities and for the same morphophysiological traits of this research, except for RDM (44%).

The analysis showed significant effect ($p < 0.01$) of progenies and light intensities for all traits. The significance of differences between the overall means for the three light intensities ($p < 0.05$, Tukey test) for the traits H, TIL, SLA, LDM, DM and RDM and genotypic values (GV) of the progenies are presented in Table 3.

The CGV/CRV ratio was greater than 1.0 for H and TIL and less than 1.0 for the other traits. This result indicates that H and TIL are important traits for studies related to reduced light and, thus, greater importance must be given to traits associated with them such as width and length of the leaf, stem height and internode size, as in the experiment carried out by Castro *et al.* (1999). According to Haynes (1980), a greater H is enough to make one leaf blade overlap another, which makes H an important characteristic for selection in *P. maximum* progenies. On the other hand, TIL is associated with leaf

area, which will determine the quantity and quality of radiation that reaches the bottom of the canopy and can activate axillary buds and, consequently, new tillers (Deregibus *et al.*, 1983).

The genotypic correlations between traits are shown in Table 2. This parameter is very important because a high genetic correlation indicates that the traits involved are controlled by the same genes or very close genes (Falconer & Mackay, 1996; Ramalho *et al.*, 2000). Therefore, as the genotypic values for H increase, greater genotypic values for SLA and DM, and lower for LDM, will be obtained simultaneously. It is expected, then, more facility in the simultaneous improvement of these traits. The increase in TIL will likely cause a decrease in the genotypic values of SLA and RDM, and with the increase in RDM, it is expected an increase in SLA and DM accumulation.

All traits are affected by light levels. In some cases, the effect is known such as the finding that photoassimilates move preferably to the growth of pre-existing tillers, instead of new ones, in shaded plants (Davies, 1981). With decreased light intensity, growth and ability of roots to absorb water and nutrients is reduced (Langer, 1972). In *Urochloa* spp., Martuscello *et al.* (2009) found a linear decrease ($P < 0.01$) in TIL and RDM with increasing shading levels.

Genotypic values of H increased with reduced light. In relation to full sun, H increased 44% and 67.4% under 50% and 70% shade, respectively (Table 3). The internode elongation in response to a decrease in incident light is a plant adaptation to maximize light interception

(Taiz & Zeiger, 1998). The same effect was found by Jank *et al.* (2005) in 28 genotypes of *P. maximum*, with H increases of 38% and 69.4% under 50% and 70% light reduction, respectively. Matta *et al.* (2009) reported for *P. maximum* that, under 75% shade, plant height is 74% higher than under other shading levels (0, 25 and 50%).

The increase in H was uniform, which is confirmed by the high genotypic correlation between progenies over the light intensities ($r = 0.88$) (Table 1). A high genetic influence on phenotype was confirmed for this character, based on the CGD of 57.96 and the high broad sense heritability (adjusted) of progeny means (= 95.81) (Table 1). Therefore, the progenies have a high possibility of repeating in the apomictic descendants the H performance obtained in this experiment, for a wide environmental range of different light conditions. Thus, the selection for a determined H performance carried out in a light intensity can be transferred to other intensities. However, there is a possibility of occurring gains for specific light intensities, hence, one can also perform selection for only one light intensity. This is possible because part of the genotype x environment interaction is complex ($CDI = 7.57$). The CGV/CRV ratio of 1.3 for H, with four replications, will result in a selective accuracy above 0.90, as it was shown by Resende & Duarte (2007). This high accuracy degree will result in high accuracy in genotype selection and favor the study and selection of H.

The progenies 1, 2, 3, and 4 had mean H above 90 cm and progenies 5 and 6 below 90 cm, in 50% light reduction (Table 3). Differences in means between these

Table 1. Estimated genetic parameters for plant height (H), number of tillers (TIL), specific leaf area (SLA), total dry matter accumulation (DM), leaf dry matter accumulation (LDM) and root dry matter accumulation (RDM) evaluated in progenies of *Panicum maximum* in three light intensities. Parameters expressed as percentage

	H	TIL	SLA	DM	LDM	RDM
Coefficient of genotypic determination (CGC)	57.96	84.19	35.66	39.60	31.05	13.95
Broad sense heritability (ajusted) of progeny means (h^2_{mg})	95.81	99.40	99.63	99.15	92.02	87.81
Genotypic correlation between the progenies over the light intensities (r)	0.88	0.98	0.99	0.98	0.79	0.71
Coefficient of genotypic variation associated with progeny (CGV)	12.40	62.36	21.15	22.41	14.16	27.27
Coefficient of residual variation (CRV)	9.56	25.70	28.32	27.45	19.83	65.43
Coefficient of determination of the effects of the interaction progenies x light intensities (CDI)	7.57	1.52	0.34	0.98	8.04	5.75

Table 2. Genetic correlations between agronomic traits in progenies of *Panicum maximum* in three light intensities

Trait	TIL	SLA	DM	LDM	RDM
H ¹	-0.27 ^{ns}	0.90**	0.89**	-0.68**	0.41 ^{ns}
TIL ²		-0.96**	-0.46 ^{ns}	0.14 ^{ns}	-0.73**
SLA ³			0.40 ^{ns}	0.48 ^{ns}	0.90**
DM ⁴				-0.32 ^{ns}	0.67**
LDM ⁵					-0.04 ^{ns}

¹H = Plant height; ²TIL = number of tillers; ³SLA = specific leaf area; ⁴DM = total dry mass accumulation; ⁵LDM = leaf dry mass accumulation; ⁶RDM = root dry mass accumulation. ^{ns} non significant, *, ** significant at 5% and 1% probability levels by the Student's t test.

two groups increased with decreasing light intensity: 9.4 cm, 17 cm and 20.5 cm for the three light intensities, respectively, because the taller progenies maintained higher potential of increasing H with reduced light. There was genetic correlation between H and SLA (0.90), DM accumulation (0.89) and LDM (-0.68) (Table 2), indicating a greater DM accumulation in the taller progenies and in the light intensities that provided higher H. These results make this trait an important component of selection indices for shade tolerance in all progenies, as indicated by the genetic variability. However, the progenies need to be separated by type of morphological development, because H is more important for the taller than the shorter-height progenies. Wong & Stur (1996) evaluated *Paspalum* genotypes with different growth habits in simulated canopies (25, 50 and 100% of full sun) and concluded that the growth habit, by itself, cannot be used as an indicator for the selection of grasses tolerant to shaded environments.

The number of tillers (TIL) decreased with shading (Table 3), which was also verified by Jank *et al.* (2006) and Paciullo *et al.* (2011). Shading changes both the intensity and the quality of incident radiation on the plants, as well as the reduction in the red:far red ratio affects the potential for tillering (Guenni *et al.*, 2008). The TIL variation had the highest genotypic influence (CGD = 84.19) and one of the largest heritabilities (= 99.4). Therefore, it showed high stability coupled with the ability to pass it on to offspring for a wide environmental range ($r = 0.98$), since the genotype x environment interaction was of the simple type. Then, the performance of TIL selected in a specific light intensity will be repeated in other intensities, because the CDI at 1.52 indicated a high genotype x environment interaction of the simple type. Furthermore, the CGV/CRV ratio of 2.42 results from a very high accuracy and strengthens the above observations. Tiller is a genetic trait, but may be greatly influenced by the environment (Langer, 1972), and our results indicate that the progenies have genetic variability for light reduction, facilitating the selection of individuals with better agronomic and qualitative forage characteristics for silvipastoral systems.

Still regarding TIL, there was the formation of two groups: progenies 1, 2, 3 and 4 with higher H means and lower TIL means and progenies 5 and 6 with lower H and higher TIL (Table 3), confirming the negative correlation between the two characters (-0.27) (Table 2). The difference between the two groups of progenies in the lower light intensities was due to the smaller decreases in tiller number of the progenies 5 and 6, indicating that the interaction light intensity x progenies was less intense for the shorter-height progenies. Pentón (2000)

observed that plants of cv. Likoni (*P. maximum*) were taller and produced less tillers with light reduction.

In breeding programs aimed at shade tolerance, it is important to determine selection indices that take into account the balance between TIL and H. Plant morphological adaptations in response to shading are expected. According to Matthew *et al.* (1995), there is a compensation effect between tillers per plant and leaf area per tiller, suggesting that the decrease in tiller number has an inverse relation with the increase in height. The ratio between the density and height of tillers affects the leaf area (Matthew *et al.*, 2001) and determines the quantity and quality of radiation that reaches the bottom of the canopy, which can activate axillary buds, producing new tillers (Deregibus *et al.*, 1983). However, the progenies need to be separated by growth type, especially in cases of important canopy traits such as H and TIL, since H will have the greatest importance in the selection indices for progenies 1, 2, 3 and 4, and TIL for the shorter-height progenies.

Genotypic values for SLA (Table 3) increased significantly with decreasing light, with means of 101.92 $\text{dm}^2.\text{g}^{-1}$, 131.78 $\text{dm}^2.\text{g}^{-1}$ and 190.96 $\text{dm}^2.\text{g}^{-1}$ for increasing levels of shading, respectively. Carlen *et al.* (1999) discussed that the increase of SLA with shading is the plant adaptation to maximize light capture and sustain growth. Baruch & Guenni (2007) and Dias-Filho (2000) also observed increases in SLA with shading of species of *Urochloa*. However, Ferreira *et al.* (2010) did not report the effect of shading (0, 25, 50 and 75%) on SLA of Tanzania grass.

SLA variation was highly influenced by genotype (CGD = 35.66) and showed high genetic correlation between light intensities ($r = 0.99$). These results suggest that the selection of this trait can be performed at any light intensity, because the genotypes selected in one light intensity will also be selected in another and have the ability to pass the trait on to offspring (= 99.63). Artificial reduction of light created a favorable condition for performing selections for biomass accumulation, which have high genetic correlations with SLA, similar to DM (0.89) and RDM (0.90).

Progenies 1, 2, 3 and 4 had the highest SLA means (155.15 $\text{dm}^2.\text{g}^{-1}$) and the highest H, while progenies 5 and 6 had the lowest SLA means (114.29 $\text{dm}^2.\text{g}^{-1}$) and the lowest TIL, which relates to the high correlations between SLA and H (0.90) and between SLA and TIL (-0.96). The difference between the group means in each light intensity was similar (42.02 $\text{dm}^2.\text{g}^{-1}$; 39.88 $\text{dm}^2.\text{g}^{-1}$ and 41.09 $\text{dm}^2.\text{g}^{-1}$) because the progenies showed similar potential for increasing SLA.

The higher TIL means of the shorter-height progenies indicate that the largest total leaf area

Table 3. Genotypic values for plant height (H, cm), number of tillers (TIL), specific leaf area (SLA, dm².g⁻¹), total dry mass accumulation (DM, g.pot⁻¹), leaf dry matter accumulation (LDM, g.pot⁻¹) and root dry mass accumulation (RDM, g.pot⁻¹) in progenies of *Panicum maximum* in three light intensities

Progenies	Full sun			50% light			30% light			All light intensities		
	H	TIL	SLA	H	TIL	SLA	H	TIL	SLA	H	TIL	SLA
1	67.35	21.01	103.67	97.45	14.18	132.82	115.08	10.65	192.36	92.91	15.37	142.93
2	67.29	20.35	124.85	98.82	14.01	153.22	113.79	11.02	214.22	92.91	15.22	164.00
3	63.62	24.88	113.82	95.70	17.26	143.45	109.02	13.07	202.05	89.22	18.48	153.05
4	67.98	23.21	121.36	95.83	15.11	150.79	113.27	12.72	209.98	92.02	17.09	160.63
5	57.99	44.06	93.16	82.02	32.81	125.46	92.47	29.69	182.73	77.77	35.49	133.79
6	56.27	71.19	54.66	77.88	60.25	84.93	92.10	52.18	144.40	75.78	61.21	94.79
Means	63.4c	34.12 a	101.92c	91.2 b	25.60 b	131.78b	105.96a	21.56c	190.96a	86.77	27.14	141.53
	DM	LDM	RDM	DM	LDM	RDM	DM	LDM	RDM	DM	LDM	RDM
1	47.20	40.45	67.60	71.79	53.48	46.54	59.78	45.68	23.73	59.65	46.31	44.71
2	53.19	32.90	54.32	77.05	47.31	42.36	65.64	43.44	17.60	65.30	41.41	37.80
3	49.59	33.33	63.71	75.81	51.46	38.54	64.94	47.09	19.85	63.48	43.93	40.09
4	84.07	47.17	64.58	111.81	61.93	49.43	97.70	56.94	24.14	97.61	54.42	44.79
5	48.18	29.18	35.52	71.21	43.45	18.24	58.58	42.20	6.64	59.39	38.70	22.01
6	56.84	30.20	38.55	83.57	52.42	26.95	71.48	49.97	13.77	70.60	44.15	27.54
Means	56.5c	35.54 c	54.05 a	81.87 a	51.68 a	37.01 b	69.69b	47.55 b	17.62 c	69.34	44.82	36.16

Means of the same trait followed by the same letter in the row are not significantly different by the Tukey test at 5% probability level.

occurred because of the increased number of leaf blades, whereas the taller progenies had larger leaf area per plant, as they increased in H. However, Pedreira (1973) reported that the most successful plant will not necessarily be the one with a higher proportion of leaves, but the one that has the leaf blades in a position more favorable to incident sunlight.

Interestingly, higher genotypic values for DM were obtained with light reduction, which were higher at 50% shading (Table 3). Some authors have found increases in DM accumulation of *P. maximum* with reduction in light intensity (Wong & Wilson, 1980; Eriksen & Witney, 1981; Castro *et al.*, 1999; Andrade *et al.*, 2004; Jank *et al.*, 2006). Wilson & Wild (1991) also attributed the higher biomass accumulation to the increased nitrogen availability that occurs in the shaded soil and stimulates the growth of grasses. However, in cultivation under forests, Carvalho *et al.* (1997) and Gutmanis *et al.* (2001) reported lower biomass accumulation.

The variation in DM was highly influenced by genotype (CGD = 39.60), high genotypic correlation with the environments ($r = 0.98$) and heritability at mean level (= 99.15) (Table 1). These conditions favor the selection for a wide environmental range, because the interaction genotype x environment was of the simple type (CDI = 0.98). Therefore, this trait can be selected in all or in only one light intensity. The CGV/CRV ratio was less than 1, but close to 1, still ensuring safe conditions for these affirmations.

Progeny 4 had the highest DM mean (97.61 g.pot⁻¹), in all light intensities and, under 50% shading, the DM mean was 111.81 g.pot⁻¹ (Table 3), which was 84% higher than the mean of the shorter-height progenies, in addition to 95.83 cm H, 150.79 dm².g⁻¹ SLA and one of the lowest TIL means (15.11 tillers). These results corroborate the report of Castro *et al.* (1999), who found a quadratic effect for DM accumulation, stem height and leaf blade length in cv. Vencedor, with the reduction in light intensity.

Progeny 6, of shorter stature, had the second largest DM accumulation under 50% shading (83.57 g.pot⁻¹), which was slightly higher than the others. To achieve this performance, it had the highest TIL mean (60.25 tillers), which was 83.63% higher than the second highest TIL mean (32.81 tillers) and the lowest SLA mean, indicating that it sustained the leaf blade thickness. Similar results were reported by Andrade *et al.* (2004) for cv. Massai (*P. maximum*) in full sun and 30, 50 and 70% of light reduction, with mass accumulation of 56.3, 57.2, 47.0 and 28.1 kg ha⁻¹.day⁻¹, respectively, indicating a greater tolerance under moderate levels of shading. Therefore, by reducing the light intensity, the taller progenies had higher DM accumulation as they had higher H and

progenies of shorter stature had higher DM accumulation, as they sustained higher TIL combined with lower SLA, which results in greater weight of the leaf blades. This result was corroborated by genetic correlations between DM accumulation and H (0.89), SLA (0.40) and TIL (-0.46) (Table 2), in addition to confirming the possibility of simultaneous improvement of SLA and H (Table 3).

The mean LDM accumulation under 50% and 70% shading in relation to full sun, was 45.41% and 33.79% (Table 3). Jank *et al.* (2006) also found increases of 52.3% and 30.4% for the same light intensities, respectively. Other authors have reported the increase of LDM accumulation with reduced light (Wong & Wilson, 1980; Carvalho *et al.*, 1995; Castro *et al.*, 1999).

The variation in LDM was highly influenced by genotype (CGD = 31.05), uniform performance over the range of environments ($r = 0.79$) and broad sense (adjusted) heritability of 92.02. Thus, this character can be selected for a wide environmental range. However, there is possibility of genetic gain for specific environments. The selection for LDM can be carried out in all light intensities, or in only one, and with high possibility to pass the performance on to the offspring.

There was a trend toward greater LDM accumulation in progenies 1, 2, 3 and 4. The difference in LDM between this group and the group formed by progenies 5 and 6, in each light intensity, was 8.77 g.pot⁻¹; 5.62 g.pot⁻¹ and 2.21 g.pot⁻¹. The shorter-height progenies had greater increase in LDM accumulation, making the performance more similar between them. Progeny 4 had the highest LDM accumulation, one of highest H means and the lowest increase in SLA, among the group of taller progenies. Progeny 6 had the higher LDM accumulation among those with lowest H, the largest increase in SLA (164.18%) and the lowest reduction in TIL.

These examples indicate that the increase in LDM should occur by increasing leaf length, which may further increase H in taller progenies and should produce a positive genetic correlation. However, this was not observed. On the other hand, the shorter-height plants had higher LDM accumulation by maintaining higher TIL means coupled to lower SLA means, indicating a greater leaf blade weight. With this trait, a positive genetic correlation was found (LDM and SLA = 0.48), although not significant, indicating that, with shading, there was increase in LDM simultaneously with the increase in SLA.

The genotypic values for RDM decreased with light reduction and, in comparison with full sun, were 32% and 67% lower for 50% and 70% shading, respectively (Table 3). Studies on *P. maximum* rooting indicate less

RDM accumulation with light reduction (Ludlow *et al.*, 1974; Eriksen & Whitney, 1981; Jank *et al.*, 2006). In the evaluation of 28 *P. maximum* genotypes, the decrease in DM in the light intensities of 50% and 70%, compared with full sun, was 41.5% and 70.3%, respectively (Jank *et al.*, 2005).

The genotypic determination in the RDM variation was very low (CGD = 13.95), the genetic correlation between the light intensities was 0.71 and the broad sense (adjusted) heritability was 87.81. Selection can be performed for a wide environmental range or specific environments, because of the moderate interaction progenies x light intensities (CDI = 5.75).

Thus, RDM can be selected for all light intensities or only one. However, Jank *et al.* (2006) concluded, in a previous experiment with 28 *P. maximum* genotypes, that the trait RDM must be selected in the environment of the target use, since the correlation between the light intensities was very low ($r = 0.438$). Although similar to the performance of other traits, a low genetic control was obtained for RDM, which may be associated with its high CRV (65.43%), which, in turn, can be related to the conditions of cultivation in pots.

In the same way as the components of shoot mass accumulation, RDM accumulation can be studied by separating the progenies 1, 2, 3 and 4 from the progenies 5 and 6. The mean of the first group was 41.85 g.pot⁻¹ and the second 24.8 g.pot⁻¹; the differences between them under full sun, 50% and 70% shading, were 26.65 g.pot⁻¹; 21.62 g.pot⁻¹ and 11.2 g.pot⁻¹, respectively. This drastic reduction under 70%, was due to the decrease in the means of genotypic values of progenies 1, 2, 3 and 4 that was greater than the decrease of progenies 5 and 6, indicating that the shorter-height progenies had greater tolerance to shading. These results may be related to the genetic correlations between RDM and H (0.41), TIL (-0.73), SLA (0.90) and DM (0.67), since in the first group, besides larger RDM accumulations, higher H, SLA and DM means and lower TIL means were recorded.

The results of this study indicate that the progenies of *P. maximum* showed greater shade tolerance under 50% light reduction, which was quantified by the traits DM, LDM and RDM, and that the shade tolerance in the taller progenies is related to the greater ability to accumulate DM and grow in H, whereas the shorter-height progenies have the ability to accumulate DM and greater ability to increase TIL. The progenies 2, 4 and 6 were the most tolerant to shading and, for progenies 2 and 4, this tolerance was due to the higher increase in H. However, the tolerance of the progeny 6 was due to maintenance of higher TIL and hence higher SLA, with light reduction.

CONCLUSIONS

For the selection of *P. maximum* genotypes to shade tolerance, it is sufficient to evaluate the traits height, tillering and biomass accumulation, in only one light intensity (50%), or also, root dry mass accumulation in different intensities, for greater realized gain.

All traits had high broad sense heritability and high genotypic correlation between the progenies over the light intensities. There is genetic difference among the progenies for the response to different light intensities, which will allow the selection for shade tolerance.

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