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Genetic gains for heat tolerance in potato in three cycles of recurrent selection

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ABSTRACT - *Practically all potato cultivars grown in Brazil are native to Europe and not fully adapted to the tropical conditions. The purpose of this study was to estimate the genetic gains of three cycles of recurrent selection for heat tolerance in potato. The base population in this study consisted of five Brazilian and five heat-tolerant clones. In the winter of 2006 and rainy growing season of 2007 103 clones were evaluated (eight clones of the base population, 29 of the first cycle, 32 and 30 of the second and third recurrent selection cycle, respectively, and four control cultivars). The genetic gains for tuber traits in both growing seasons were 37.8 % (yield), 13.0 % (weight), 32.4 % (percent of large tubers), 0.8 % (tuber specific gravity) and 16.6 % (general tuber appearance). The percentage of physiological disorders (second-growth tubers and cracking) was also reduced by selection.*

Key words: Solanum tuberosum *L.; stress; heat; breeding.*

INTRODUCTION

In the tropics and subtropics heat is a major limiting factor in potato cultivation. However, there are reports of the existence of genetic variability for heat tolerance (Tai et al. 1994, Menezes et al. 1999), which could be exploited in breeding programs. The trait heat tolerance is controlled by several genes, making the selection of tolerant plants in breeding programs rather difficult. In the improvement method of recurrent selection, the frequency of favorable alleles in a population is increased by the selection of genotypes that are superior to the base population and by the subsequent recombination of the best genotypes for the subsequent selection cycle.

The recurrent selection method is not used very often in potato improvement, but some researchers have applied it successfully (Plaisted and Peterson 1963, Gautney and Haynes 1983, Sanford and Ladd Jr 1987, Haynes 2001, Bradshaw 2005). Plaisted and Peterson (1963) worked with recurrent selection to increase the tuber specific gravity. After two selection cycles, the tuber specific gravity increased 0.004 units in the first cycle in the mean of two locations, and 0.005 units in the mean of two seasons. Gautney and Haynes (1983) used recurrent selection with a view to adapt the diploid potato varieties *S. tuberosum* ssp. *phureja* and *S. stenotomum* to heat. At the end of the first cycle of recurrent selection for phenotypic traits, they reported a gain of 3 % in terms of plant survival, 15 % in tuberization and 27 % in tuber yield. Sanford and Ladd Jr (1987) used recurrent selection to increase resistance to the potato leafhopper *Empoasca fabae*. At the end of seven selection cycles, the level of nymph infestation was reduced

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by 75 % and plant damage by 45 %. Haynes (2001) used recurrent selection to study the variance components of yield and tuber specific gravity in a diploid population. The author reported that gains for specific gravity in this population are possible, but the estimated variance for tuber yield decreased, indicating that the yield potential might be quickly reached.

A recurrent selection program for several traits was conducted by the Scottish Crop Research Institute (SCRI - Scotland) in three-year cycles (Bradshaw 2005). The program was initiated with biparental crosses of 10 clones resistant to potato late blight (*Phytophthora infestans*) with 12 clones resistant to cyst nematode (*Globodera rostochiensis*), resulting in group A. Group B was established by crossing the 10 late blight-resistant clones with 14 other clones resistant to viruses and group C resulted from crosses of the 12 cyst nematode-resistant with the 14 virus-resistant clones. In the seedling generation selection was performed based on visual aspects such as tuber appearance, resistance to late blight and cyst nematode. At this stage, families with poor performance for these traits were discarded and selection within families performed in the next step. The clones selected visually within families were recombined to form the population of the following cycle and multiplied for further evaluation in the field for tuber quality. In the first selection cycle 108 clones with multiple resistance were detected (Bradshaw 2005). In the second cycle selected clones were crossed between the groups (AxB, AxC and BxC). Another progeny test was performed with the clones in the seedling generation and field evaluation. At the end of the second cycle 27 clones were selected and crossed for the third cycle. A new selection of seedlings in the field resulted in 36 clones that were evaluated again for tuber quality and disease resistance. The selection gains for the trait set were 28 % in the first cycle, 32 % in the second and 41 % in the third cycle (Bradshaw 2005). The 24 best selected clones in terms of tuber appearance, resistance to late blight and to cyst nematode were compared to the original 39 parents and 43 random clones of the population in the third selection cycle. None of the 39 parents met the selection criteria required, whereas the means of the 24 selected clones for the separate traits were very close to those of the best parent, the source of the target traits.

Unlike the authors mentioned above, Santa Cruz et al. (2009) applied recurrent selection without success for resistance to early blight (*Alternaria solani*) in diploid potatoes, despite the high broad and narrow-sense heritability (0.75 ± 0.06 and 0.69 ± 0.29, respectively). The authors ascribed the failure of recurrent selection to the focus of selection on agronomic traits and the association between earliness and susceptibility, so that selection of clones with better agronomic traits implied selection for susceptibility.

The purpose of this study was to estimate the genetic gain in three cycles of recurrent selection for heat tolerance in potato (*Solanum tuberosum* L.).

MATERIAL AND METHODS

The base population for recurrent selection consisted of five Brazilian genotypes (Aracy, Baronesa, Itararé, EPAMIG 76-0526, and EPAMIG 76-0580) and five heat-tolerant genotypes (Desirée, LT-7, LT-8, LT- 9, and DTO-28). The clones LT and DTO were released by the International Potato Centre, Peru (CIP) as heat-tolerant and Desirée is a Dutch cultivar. These 10 genotypes were crossed, resulting in the CBM population selected for heat tolerance and high tuber dry matter (Menezes et al. 2001). The CBM population was considered the first cycle of recurrent selection, of which 13 clones were used, together with the control cultivars Atlantic and Chiquita to generate the population of the second selection cycle, called RS1. Crosses among the 13 CBM clones and cultivars 16 RS1 families were produced, with a total of 2500 seedlings. After field multiplication (first clone generation - C1) 1400 clones were harvested in the second generation (C2) of which 150 with superior tuber appearance were evaluated in the winter growing season 2003. In this experiment 50 third-generation (C3) clones were assessed in the rainy season of 2004. The yield of population RS1 was evaluated again in the winter and rainy growing seasons, when 32 fourth-generation (C4) clones with heat tolerance and good agronomic performance were selected.

The population of the third recurrent selection cycle (RS2) was obtained by the recombination of 32 RS1 clones, 5 ESL clones (Lambert and Pinto 2002) and the cultivar Atlantic, together with 15 open-pollinated RS1 families. A total of 197 clonal families and approximately 6000 seedlings were the result. The first-clone generation (C1) was multiplied in the field (2000 clones) from which 368 second-generation clones (C2) were selected. In the evaluation of the C2 generation in the rainy season 30 clones of the third generation (C3) with heat tolerance and good agronomic performance were selected.

In the winter 2006 and rainy season of 2007 the clones of the three recurrent selection cycles were evaluated to estimate the genetic gains. The evaluations were conducted at the experimental site of the Department of Biology - Ufla, Lavras, MG. A total of 103 clones were evaluated, eight of the base population, 29 of the CBM population, 32 of population RS1, 30 of RS2 and four control cultivars (Ágata, Asterix, Atlantic, and Monalisa).

The experiments were conducted in a randomized block design with three replications, in plots with five plants spaced 0.30 x 0.80m. The following traits were evaluated: tuber yield (g plant^{-1}), percentage of large tubers (transversal diameter > 45 mm), mean weight of large tubers (g), tuber specific gravity and general tuber appearance (grade 1 = poor appearance to 5 = excellent appearance). In the rainy season, the percentage of large tubers with physiological disorders (second-growth tubers and cracking) were evaluated.

In these experiments, the best eight clones of each population CBM, RS1 and RS2 were selected for comparison with eight clones of the base population of recurrent selection. The eight best clones of each population were classified by the rank-sum index of Mulamba and Mock (1978) considering the tuber yield, the percentage of large tubers, mean weight of large tubers, tuber specific gravity and the grade of tuber appearance in the winter experiment. In the rainy growing season, aside from the above traits, the percentage of cracked tubers and second-growth tubers was included in the clone classification.

Estimates of genetic parameters were computed using software Genes (Cruz 2001) and the selection gains in the cycles for the best eight clones of populations CBM, RS1 and RS2 and the eight clones of the base population were calculated by the expression: $SG(\%) = \frac{ds \cdot h_a^2}{\bar{X}_o} \cdot 100$, where

SG: is the expected gain with selection for the trait considered;

ds: selection differential, calculated as the difference between the trait mean of the eight selected clones and the mean of eight clones of the previous cycle ($\bar{X}_o$);

h_a^2: broad-sense heritability at the mean clone level, for the trait considered.

In the combined analysis h_a^2 to estimate the gain was at the mean clone level of both environments, for the trait considered.

RESULTS AND DISCUSSION

The climatic conditions in the winter growing season (2006) were adequate for potato cultivation with temperatures below 20 ºC in approximately 65 % of the growing season and for a short time (10 %) the daily temperatures were above 25 °C. The opposite occurred in the rainy season, where temperatures were above 20 ºC for about 55 % of the growing season and even reached levels higher than 25 °C in 25 % of this period. Haverkort (1990) comments that potato is better adapted to high-altitude tropical regions where mean daily temperatures are between 15 and 18 ºC. Menezes at al. (1999) reported that under the same climatic conditions as in this study, but at higher temperatures, potato leaf development is favored and tuberization delayed.

In the winter growing season (2006) there were significant differences between clones for all traits (Table 1). The mean tuber yield of 1211.5 g plant^{-1} was high, due to the favorable temperature. Mean tuber specific gravity, which is closely correlated with dry matter content, was 1.0814, indicating a high suitability of the clones for tuber processing in the form of frying. The cultivars for household consumption (Ágata and Monalisa) have very low values (around 1.060) while some of the cultivars used in industry as Asterix (straws) and Atlantic (chips) have values between 1.070 and 1.080.

The mean grade of tuber appearance of the experimental clones was 2.38, but 2.33, 2.0, 3.66, and 2.66 for the controls Asterix, Atlantic, Ágata, and Monalisa, respectively. These grades were relatively low due to the soil type (Clayey Texture Typic Dystroferric Red Latosol - Oxisol) (Embrapa Solos 2006). This soil grows reddish tubers, with a skin that is rougher than usual. However, in the winter growing season the tuber appearance was not affected by heat stress that would cause physiological disorders. Heritability estimates ranged from 50.7 % to 80.1 % and the ratios CV_g/CV_e were high, indicating favorable conditions for selection.

In the rainy season (2007) the differences between clones for all traits were also significant except for percentage of second growth tubers (Table 2). The growing conditions were unfavorable due to the high temperatures, causing a reduction in the trait means of the clones compared to the winter experiment. The mean tuber yield was reduced by 56.9 % due to reductions in the percentage of large tubers (26.4 %) and tuber weight (20.4 %). The mean grade for tuber appearance also decreased by 7.1 %, due to the high temperatures which, in turn, increased the incidence of physiological disorders. In histological studies in the periderm of cultivar Nicola, Ginzberg et al. (2005) found that the arrangement of the periderm tissues is disarranged when

Table 1. Summary of analysis of variance for tuber yield, percentage of large tubers, mean weight of large tubers, tuber specific gravity and tuber appearance. Winter growing season (2006)

SV	df	Mean squares				
		Tuber yield (g plant^{-1})	% of large tubers	Mean weight of large tubers (g)	Specific gravity	Tuber appearance
Clones	102	367228.61**	8.32 x 10^{-2}**	2014.50**	1.81 x 10^{-4}**	0.75**
Error	204	73113.90	2.04 x 10^{-2}	613.12	0.35 x 10^{-4}	0.37
Mean		1211.48	69.77	142.72	1.0814	2.38
CV_e (%)		22.31	20.45	17.34	0.55	25.54
b		1.16	1.01	0.87	1.17	0.58
σ^2_G		98038.23	2.09 x 10^{-2}	467.12	0.48 x 10^{-4}	0.13
h^2_a (%)		80.09	50.68	69.56	80.44	50.35

** significant at 1 % probability by the F test.
b = CV_e/CV_g.

Table 2. Summary of the analysis of variance for tuber yield, percentage of large tubers, mean weight of large tubers, tuber specific gravity, tuber appearance, percentage of cracked tubers and percentage of second-growth tubers. Rainy growing season (2007)

SV	df	Mean squares						
		Tuber yield (g plant^{-1})	% large tubers	Mean weight of large tubers (g)	Specific gravity	Tuber appearance	% cracked tubers (x 10^{-2})§	% second growth (x 10^{-2})§
Clones	102	76856.04**	11.81x10^{-2}**	1376.15**	2.17x10^{-4}**	0.63**	0.63**	0.23
Error	204	37179.95	3.11x10^{-2}	467.58	0.50x10^{-4}	0.34	0.31	0.17
Mean		522.35	51.33	113.66	1.0782	2.21	3.4	4.14
CV_e (%)		36.91	34.36	19.02	0.66	26.18	4.09	4.07
b		0.60	0.97	0.80	1.05	0.54	0.52	0.34
σ^2_G		13225.36	0.03 x 10^{-2}	302.85	0.56 x 10^{-4}	9.68 x 10^{-2}	4.7 x 10^{-4}	2.01 x 10^{-4}
h^2_a (%)		51.62	73.65	66.02	52.60	46.32	45.00	25.92

** significant at 1 % probability by the F test.
§ Data transformed by $\sqrt{x+1}$.
b = CV_e/CV_g.

the tubers are grown at high temperatures. Under such conditions, pectin and hemicellulose deposition in the suber cells increases, resulting in greater adhesion between cells (Okazawa and Iriuda 1980). As the tubers grow, cracks appear on the skin due to the strong adhesion between cells, making the tuber surface rougher.

Tuber specific gravity was reduced by 0.0032 units and was not greater due to the heat tolerance of most of the experimental clones. The heat stress caused physiological disorders in the tubers and the means of percentage of cracked and second-growth tubers were 3.40 and 4.41% respectively.

Estimates of heritability were also lower compared to the winter experiment, as well as the ratio CV_g/CV_e. This shows the great difficulty of performing selection under rather unfavorable environmental conditions, as pointed out by some authors (Cecarelli 1994, Lambert et al. 2006). On the other hand, the tuber specific gravity ratio CV_g/CV_e was higher than the unity, indicating that selection for this trait could be successful, even at high temperatures. Tai et al. (1994) used the criterion tuber dry weight, which is closely correlated with tuber specific gravity, in a selection index, as indicator of heat tolerance.

The combined analysis of the winter and rainy-season experiments is shown in Table 3. The differences between clones and the clone x growing season interaction were significant for all traits. The existence of interaction indicates the different clone performance in the two growing seasons. In general, the heritability and the ratios CV_g/CV_e were lower than the estimates obtained in each season and show that clone selection based on the mean of the two growing seasons (winter and rainy) would be less efficient than selection in each environment. However, Lambert et al. (2006) showed that selection at high temperatures favors specifically adapted clones that do not respond to cooler temperatures. It is important to

Table 3. Summary of combined analysis of variance for tuber yield, percentage of large tubers, mean weight of large tubers, tuber specific gravity and tuber appearance, of the winter (2006) and rainy (2007) growing seasons

SV	df	Mean squares				
		Tuber yield (g plant^{-1})	% of large tubers	Mean weight of large tubers (g)	Specific gravity	Tuber appearance
Clones (C)	102	292421.84**	13.60 x 10^{-2}**	2330.79**	3.3 x 10^{-4}**	0.92**
C x Seasons	102	182650.06**	6.31 x 10^{-2}**	1155.95**	0.7 x 10^{-4}**	0.48
Error	408	55807.89	2.63 x 10^{-2}	544.13	0.4 x 10^{-4}	0.38
Mean		875.38	60.76	128.54	1.0799	2.30
CV_e (%)		26.98	26.70	18.14	0.60	26.67
b		0.57	0.68	0.60	1.00	0.44
σ^2_G		18295.29	1.22 x 10^{-2}	195.80	0.4 x 10^{-4}	0.07
h^2_a (%)		37.53	53.62	50.40	77.73	48.25

** significant at 1 % probability by the F test.
b = CV_e/CV_g.

mention that producers normally do not grow potatoes under completely unfavorable temperature conditions, but these may occur during the crop cycle. Thus, heat-tolerant clones that also respond well to lower temperatures would be desirable.

The means of eight clones selected by the index of Mulamba and Mock (1978) in each cycle of recurrent selection, as well as the eight clones of the base population and the four cultivars are presented in Table 4. The superiority of the selected experimental clones and cultivars over the base population as well as the check cultivars for most traits was outstanding. Tuber appearance was the only trait without considerable improvement by selection compared to the controls, particularly compared with tubers of cultivar Agata that have a light yellow, smooth and shiny skin and are greatly appreciated by consumers.

The mean tuber yield of the selected clones was over 1000 g plant^{-1}, evidencing the high potential even at high temperatures. The high specific gravity of these clones (> 1.080) is also noteworthy for making them suitable for the potato processing industry (potato chips, straws and frozen pre-fried). At high growth temperatures, the specific gravity is usually reduced to values that impede the production of high-quality raw material

The genetic gains in cycles of recurrent selection based on the mean of two growing seasons are presented in Table 5. In the first cycle of recurrent selection the gains between CBM clones and clones of the base population were estimated. A gain for all traits was observed, ranging from 0.48 % for tuber specific gravity to 40.8 % for percentage of large tubers. Although the estimated specific gravity gain seems small, it represents about 0.005 units, corresponding to approximately 1 % of tuber dry matter; this is certainly an important accomplishment in potato for the frying industry. Gains in specific gravity were similar to those reported by Plaisted and Peterson (1963) in two cycles of recurrent selection. The yield gain was more a result of the increased percentage of large tubers than of tuber weight. A marked improvement in tuber appearance was also observed, which is an extremely important trait for the fresh potato market.

The gains in the second and third cycles of recurrent selection were small or even negative (Table 5). These results may be a consequence of the inclusion of heat-susceptible clones as well as open-pollinated families. The inclusion aimed to broaden the genetic basis of families, particularly in terms of tuber specific gravity, which is strongly affected by heat. In cycle 3 (RS2), 15 open-pollinated half-sib families were also included. The open-pollinated seeds are predominantly produced by selfing that reaches rates of 70 – 80 % (Glendinning 1976, Brown and Huaman 1984), resulting in inbreeding. It should also be noted that no care was taken to avoid crosses between plants of the same family in the recombination of RS1 clones, which may have led to some level of inbreeding as well. Inbreeding in tetraploid is more pronounced than in diploid species and highly detrimental to potato vigor and yield (Mullin and Lauer 1966, Glendinning 1976, Momenté and Pinto 1995) and, therefore, these families may have prevented further gains in these cycles.

In the three selection cycles together, the gains were substantial, ranging from 0.83% for tuber specific gravity to 37.85 % for yield (Table 5). The positive result is that even in the multiple trait selection, the population mean was not reduced, compared to the parental means (Table 4). In multiple trait selection, the progress is slower at the

Table 4. Means of the eight best clones of each cycle of recurrent selection based on the index of Mulamba and Mock (1978) in the combined analysis of the winter (2006) and rainy (2007) growing seasons

Cycles of recurrent selection	Selected clones	Tuber yield (g plant^{-1})	Mean weight of large tubers (g)	% large tubers	Tuber specific gravity	Tuber appearance
Base Population	Aracy	847.92	109.09	53	1.0811	2.33
	Baronesa	721.81	140.84	47	1.0668	1.75
	Desireé	511.39	90.40	33	1.0697	1.67
	LT 9	358.47	102.36	40	1.0694	2.08
	LT 7	598.96	117.01	51	1.0753	1.92
	LT - 8	733.17	100.00	20	1.0838	1.17
	Itararé	467.78	188.94	47	1.0749	1.33
	Epamig 76-0580	464.58	93.47	44	1.0668	1.67
		588.01	117.76	41.88	1.0735	1.74
Cycle I	CBM 24-06	1302.08	166.5983	80	1.081	2.17
	CBM 4-48	1231.04	145.68	78	1.0777	2.67
	CBM 10-27	1200.00	162.9967	75	1.0809	2.25
	CBM 7-78	1071.19	139.7467	82	1.0813	2.33
	CBM 9-10	1240.83	135.4183	71	1.0847	2.17
	CBM 14-18	1230.00	144.03	75	1.0809	2.17
	CBM 11-10	1045.49	138.6983	63	1.082	2.83
	CBM 15-25	1045.14	143.96	84	1.0725	2.33
Mean		1170.72	147.14	76.00	1.0801	2.37
Cycle II	RS1 7-42	1012.50	146.28	79	1.0933	2.58
	RS1 7-04	973.12	147.38	85	1.0902	2.50
	RS1 7-40	1062.50	176.10	82	1.0805	2.42
	RS1 7-03	987.15	136.76	77	1.0886	2.50
	RS1 4-02	931.25	159.40	71	1.0900	2.25
	RS1 7-16	1032.64	150.45	64	1.0844	2.17
	RS1 7-36	923.89	146.09	76	1.0821	2.75
	RS1 7-08	1004.51	144.45	76	1.0762	2.92
Mean		990.95	150.86	76.25	1.0857	2.51
Cycle III	RS2 9-2	1262.50	153.75	68	1.0918	2.25
	RS2 6-9	1035.76	122.78	82	1.0894	2.67
	RS2 26-11	1439.58	157.24	79	1.084	2.00
	RS2 57-2	1129.58	142.95	74	1.0887	2.08
	RS2 50-2	1031.04	161.88	59	1.0809	2.83
	RS2 21-2	1441.67	139.53	65	1.0792	2.33
	RS2 50-4	1080.21	162.25	77	1.0751	2.17
	RS2 24-3	1027.50	129.92	48	1.0889	2.42
Mean		1180.98	146.29	69.00	1.0848	2.34
Controls	Ágata	687.29	108.79	40	1.0592	3.25
	Asterix	683.05	150.15	50	1.0755	2.25
	Atlantic	904.44	114.29	54	1.0732	1.83
	Monalisa	991.67	164.83	72	1.0729	2.67
Mean		816.61	134.52	54.00	1.0702	2.50

individual plant level, but this reduction is offset by a better distribution of positive gains in other traits (Cruz and Regazzi 1997). Bradshaw et al. (2003) found modest gains in recurrent selection for multiple traits, but stated that after three selection cycles for disease resistance and quality, the advantage over the previously used method in the breeding program was already considerable. The reason is the greater probability of detecting superior plants for the target trait set in subsequent recombinant generations. The genotype x environment interaction (Table 3) may also have limited the possibility of even greater gains, but as mentioned above, the heat-tolerant

Table 5. Estimates of gains (%) of cycles of recurrent selection in the winter (2006) and rainy growing sesaons (2007)

Population	Tuber yield (g plant^{-1})	Mean weight of large tubers	% Large tubers	Tuber specific gravity	Tuber appearance
Cycle 1					
CBM–Base Pop	37.19	13.38	40.80	0.48	17.19
Cycle 2					
RS1–CBM	-5.76	1.36	0.66	0.40	3.07
Cycle 3					
RS2–RS1	7.20	-1.62	-5.24	-0.05	-3.27
Total					
RS2–Base Pop	37.85	12.99	32.40	0.83	16.64

clones must be responsive to lower temperatures, since growers always try to cultivate potatoes under the most favorable conditions.

In the case of the percentage of tubers with physiological disorders (cracking and second growth), the gains were only estimated for the rainy season, when temperatures are higher and the problem more severe. The gains were high, with a considerable reduction in the mean of the base population. The reduction in percentage of second-growth tubers was 37.69 % and 55.38 % in percentage of cracked tubers.

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Ganhos genéticos com três ciclos de seleção recorrente visando a tolerância ao calor em batata

RESUMO - *As cultivares de batata plantadas no Brasil são praticamente todas de origem européia e não são completamente adaptadas às condições tropicais do Brasil. O objetivo deste trabalho foi estimar os ganhos genéticos com três ciclos de seleção recorrente visando à tolerância ao calor em batata. A população base deste estudo foi formada por cinco clones brasileiros e cinco clones tolerantes ao calor. Nas safras de inverno de 2006 e das águas de 2007 foram avaliados 103 clones, sendo oito da população base, 29 do primeiro ciclo, 32 do segundo e 30 do terceiro ciclo de seleção recorrente e mais quatro cultivares testemunhas. Os ganhos genéticos para caracteres dos tubérculos na média das duas safras foram de 37,8 % (produtividade), 13,0 % (peso médio), 32,4 % (porcentagem de graúdos), 0,8 % (peso específico) e 16,6 % (nota de aparência). Observaram-se, ainda, redução na porcentagem de desordens fisiológicas (embonecamento e rachaduras).*

Palavras-chave: Solanum tuberosum L.; *estresse; alta temperatura; melhoramento genético.*

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