Crop Breeding and Applied Biotechnology 6:185-193, 2006
Brazilian Society of Plant Breeding. Printed in Brazil

ARTICLE

Potato improvement for tropical conditions: II. Selection indices and efficiency of indirect selection

Eduardo de Souza Lambert[1], César Augusto Brasil Pereira Pinto[2*], and Cícero Beserra de Menezes[3]

Received 11 July 2005

Accepted 29 November 2005

ABSTRACT - *This study evaluated the efficiency of selection indices that can contribute to potato clone selection under favorable and stressful conditions as well as the possibility of indirect selection for heat tolerance. Among the selection indices, the arithmetic and geometric means and index 4 were the most appropriate. The susceptibility index and percentage of yield reduction indicate only specifically adapted clones. Indirect selection for heat tolerance is not suitable in view of the low correlation coefficient among clone means in the environments. Selection based on the overall environment mean is more fit to select broadly adapted genotypes. In general, clones that performed best under stress conditions and presented heat tolerance were specifically adapted, in spite of low performance means under favorable conditions. Well-adapted genotypes to both stress and favorable conditions can however be selected.*

Key words: *Solanum tuberosum* L., heat tolerance, genetic improvement.

INTRODUCTION

Improvement program strategies generally focus on the selection of broadly adapted genotypes and the environments considered ideal for selection are representative of the population from environments within the scope of the program (Blum 1988).

In the case of selection for favorable conditions, the strategy of evaluation in cultivation-near environments has been successful and in most improvement programs this is the way selection is performed (Cecarelli et al. 1998). However, in the case of selection for stress conditions, several questions are open concerning the strategies to be used. According to Cecarelli at al. (1998), even when targeting stressful environments, selection in improvement programs is conducted under favorable conditions. The reason is that under conditions of higher yield, the control of environmental variation is more effective, with a clearer expression of the genetic differences, resulting in higher heritabilities than under stress conditions. Furthermore, genotypes with a high yield potential and selected under ideal conditions generally perform better than genotypes selected under adverse conditions, not only in favorable but also under moderate stress conditions (Duvick 1992).

[1] Embrapa Soja, Campo Experimental de Balsas, Rodovia BR 230, km 02, C. P. 131, 65.8000-000, Balsas, MA, Brasil
[2] Departamento de Biologia, Universidade Federal de Lavras, C. P. 3037, 37.200-000, Lavras, MG, Brasil. *E-mail: cesarbrasil@ufla.br
[3] Sakata Seed Sudamerica, km 10, C. P. 427, 12.906-840, Bragança Paulista, SP, Brasil

Still, Cecarelli (1994) claims that few studies have been carried out in marginal areas under more drastic stress. The main cause for the lack of progress with selection in such conditions is the conduction of selection under the favorable environmental conditions of experimental stations or in environments of less pronounced stress. The hypothesis for the low genetic gains frequently observed under diverse stress conditions (high temperatures, water stress, acid soils) is that the cultivars generally labeled as broadly adapted are rather specifically adapted to ideal or near-optimum conditions of crop development (Cecarelli 1994). Selection in ideal conditions has rarely achieved success for extreme stress conditions, as stated by Whitehead and Allen (1990) and Singh et al. (1995).

In the case of selection for stress conditions, the genotype x environment interaction is of basic importance and the breeder is greatly challenged with the problem of selecting genotypes for each environment type. To improve selection efficiency one can use the mean of the favorable and unfavorable environments to achieve a desirable performance in both conditions (Cecarelli et al. 1998). Specifically for stress conditions, however, direct selection is more effective in the same environment than selection for the mean of both favorable and unfavorable environments. Other studies conducting segregating populations recommend alternating selection in favorable and stress conditions, which is effective to select genotypes that perform well in both conditions (Calhoun et al. 1994, Kirigwi et al. 2004).

Several selection indices are indicated in the literature to support the selection of genotypes evaluated in favorable and stress cultivation conditions (Abebe et al. 1998, Kirigwi et al. 2004, Parentoni et al. 2001, Yadav and Bhatnagar 2001). This becomes necessary, since in the evaluation of high numbers of genotypes a large volume of data needs to be analyzed and interpreted which affects the overview of the results. The trend is therefore to join information in a single selection index.

Improvement of potato for tropical conditions aims at the selection of genotypes with less reduced tuber yields under high temperatures. Elevated temperatures have several negative effects on the crop, such as the reduction of assimilate partitioning to the tubers, delayed initiation of tuberization, reduction in the tuber dry matter content, and increase in the incidence of tubers with physiological disorders.

The objective of the present study was to evaluate indices that could contribute to the selection of potato clones evaluated under stress and favorable cultivation conditions, along with an evaluation of the best selection strategies and the viability of indirect selection for heat tolerance.

MATERIAL AND METHODS

Data derived from the experiments described by Lambert et al. (2006), installed in different locations and planting periods in the South of Minas Gerais between 1999 and 2002, were used here.

Fifty-one clones derived from crossings of Brazilian cultivars and heat-tolerant clones from CIP (Centro Internacional de La Papa) based on 36 biparental crossings, described by Menezes et al. (2001), were evaluated. The traits we evaluated were tuber yield (with low heritability, $h^2 = 0.35$ percentage of large tubers (heritability value considered intermediate in this study, $h^2 = 0.80$) and tuber specific gravity (high heritability, $h^2 = 0.87$). The selection indices presented in Table 1 were applied, based on the clustering of the experiment means under high temperature stress conditions in the rainy summer season and under favorable conditions of winter cultivation. We emphasize that the heat stress temperatures considered here are normal in the summer in Lavras, where mean maximum temperatures are 28.5 ºC, and mean minimum temperatures 16.5 ºC. Lavras lies in the south of the state of Minas Gerais (lat 21º 14' S, long 45º 00' W, alt 910 m asl).

To identify the best selection indices we estimated the coefficients of correlation between the indices of the clones and the means of the respective clones in the trials under stress conditions, in favorable conditions and in the trial means. The genetic progress expected with selection was also estimated by the expressions proposed by Cruz and Carneiro (2003), as shown below.

Direct progress - selection based on the performance in one environment (i) and progress in the same environment (i)

$$GS_{(i/i)} = \frac{k\hat{\sigma}^2_{Gi}}{\hat{\sigma}_{Pi}}$$

Table 1 - Selection indices (SI) used to identify superior potato genotypes based on the evaluation under stress conditions of high temperatures, in the summer, and in favorable cultivation conditions in the winter

Indices	Description
SI 1 = Ai/Bi	where Ai: mean of the genotype i under stress and Bi: mean of the genotype i in favorable condition
SI 2 = (Bi-Ai)/mi	where m is the mean of the genotype i in all environments of evaluation
SI 3 = Ai/Bi x Ai/T	where T is the yield of the genotype with best performance for the trait under stress
SI 4 = (Ai x Bi)/(A x B) in	where A is the mean of all genotypes under stress and B the mean of all genotypes favorable condition
SI 5 =[(Ai X Bi)/(A X B)][Ai/A]	(terms defined above)
SI 6[1] = (1-Ai/Bi)/(1-A/B)	" "
SI 7 = $\sqrt{Ai * Bi}$	" " (geometric mean)
SI 8[2] = 100 [1-(Ai/Bi)]	" " (percentage of reduction in the trait)

Source: Adapted from Parentoni et al. (2001); [1] Fischer and Maurer (1978); [2] Abebe, Brick and Kirkby (1998)

where

k is the standardized selection differential , in this case 1.755 (i=10%)

$\hat{\sigma}_{Pi}$ is the estimate of the phenotypic standard deviation among clone means in environment i

$\hat{\sigma}^2_{Gi}$ is the estimate of genetic variance among clones in environment i

Indirect progress (correlated responses) - selection based on the performance in one environment (i) and progress in another environment (j)

$$GS_{(i/j)} = \frac{kCov(G_{ij})}{\hat{\sigma}_{Pi}}$$

where

$\hat{\sigma}_{Pi}$ is the estimate of the phenotypic standard deviation among clone means in the selection environment i;

$Cov(G_{ij})$ is the estimate of genetic covariance among clone means in the environments i (of selection) and j (of response).

Selection in one environment (i) and progress in the mean of environments (m)

$$GS_{(i/m)} = k\frac{Cov(P_i\overline{M}) - \frac{\sigma^2_{Ei}}{a.r}}{\hat{\sigma}_{Pi}}$$

where

$\hat{\sigma}_{Pi}$ is the estimate of the phenotypic standard deviation among clone means in environment i

$Cov(P_i\overline{M})$ is the covariance between clone means in environment i with the means of the respective clones in all environments. This covariance is of phenotypic nature

σ^2_{Ei} is the residual variance in environment i

a is the number of environments

r is the harmonic mean of the number of replications of the experiments

Selection based on the mean of environments (m) and progress in individual environments (j)

$$GS_{(m/j)} = k\frac{Cov(P_j\overline{M}) - \frac{\sigma^2_{Ej}}{a.r}}{\hat{\sigma}_{Pij}}$$

where

$\hat{\sigma}_{Pij}$ is the estimate of the phenotypic standard deviation among clone means in the environments (compare the other terms as defined above).

Selection based on the environment mean and progress in the environment mean

$$GS_{(ij/ij)} = \frac{k\hat{\sigma}^2_{Gij}}{\hat{\sigma}_{Pij}}$$

where $\hat{\sigma}_{Pij}$ is the estimate of the phenotypic standard deviation among clone means in the environments;

is the estimate of the genetic variance among clones in the environments, obtained based on the joint analyses of variance for the traits.

The efficiency of indirect selection (EIS) is given by:

$$EIS = \frac{GS_{(i/j)}}{GS_{(j/j)}}$$

where

$GS_{(i/j)}$ is the gain with selection in environment j from performance-based selection in environment i

$GS_{(j/j)}$ is the gain with selection in environment j from performance-based selection in environment j

RESULTS AND DISCUSSION

The summary of the analyses of variance and estimates of the components of variance are given in Lambert et al. (2006). The means of the traits in the evaluations under stress were quite low, with a 58% reduction in tuber yield, 25% in the percentage of large tubers and 1.08% in tuber specific gravity, compared with the means of the favorable environments. There was a low non-significant correlation between the clone means in the stress condition with the means of the respective clones in the favorable condition which was -0.04 for tuber yield and 0.24 for percentage of large tubers. For tuber specific gravity, this correlation was higher and significant as well, with a value of 0.65.

Table 2 displays the correlation coefficients between the indices obtained for the clones and the means of the respective clones in stress condition, in the absence of stress and with the mean of the environments. Only indices 4 and 5, and the geometric and arithmetic means, presented positive correlation simultaneously with all considered environmental means for tuber yield and percentage of large tubers.

For tuber specific gravity, index 3 presented a positive correlation coefficient with the mean in the stress condition but not in the absence of stress (Table 2). The indices 1 and 3 attribute greater weight to the mean of the environments with stress, so genotypes with low performance in the best environments are selected, which can be observed by the negative correlation with the means in these latter environments (Table 2). Even though the correlation between index 3 with the mean in the absence of stress had been positive for tuber specific gravity, it was of low magnitude and not significantly different from 0 by the t test.

Indices 2 and 6 present the same problem as the previous indices, of selecting low-performing genotypes in the best environments, however in the opposite sense, since for the selection with indices 2 and 6 the genotypes with the smallest values are considered. Note the high negative correlation of these indices with the means under stress and positive, but low, with the means of the favorable environments for tuber yield (Table 2). For the other two traits, the correlations with the indices were lower, but with the same significance as above. These results are similar to those found by Parentoni et al. (2001) for maize.

Indices 4 and 5 seem to be the most recommended as they presented positive correlation with all considered means, selecting clones with good performance in the stressful as well as stress-free environments. However, the correlations between these indices and the mean in the absence of stress were lower for tuber yield (Table 2). Index 5 was proposed by Parentoni et al. (2001), as indicated for the selection of maize genotypes evaluated under different soil aluminum levels.

The percentage of reduction of the trait mean under stress (PR) should not be used as selection criterion, once it presented similar correlations to indices 2 and 6 (Table 2). According to Abebe et al. (1998), the PR and susceptibility index (index 6) evaluate only the change of performance of the genotypes among the environments and should not be indicated as reliability measures to describe the performance in the environments. These two indices presented negative and low correlation with the environmental mean. Clarke et al. (1992) concluded that the susceptibility index (index 6) did not differentiate drought-tolerant genotypes from those with a low yield potential.

Some clones with low percentage of yield reduction presented low yield mean in the stress-free environments (Table 3). Taking the concepts proposed by Hall (2003) into account and considering only the trait tuber yield, clone CBM 2-21 can be classified as heat-tolerant, because it presented the smallest yield loss in relation to the mean in the favorable environments, and resistant, since its mean exceeded that of the other clones in the environments under stress. Nevertheless this clone is adapted to stress conditions only, because it did not respond to improved environment, presenting a low mean under favorable conditions (Table 3). Clone CBM 2.06, on the other hand, presented high yield in the stress-free environment, but was among the least productive in the environment under stress, with a high percentage of reduction in the trait. This clone can be classified as a genotype adapted

Table 2. Coefficients of correlation between the indices and the mean of each clone in the environments with and without stress for tuber yield, percentage of large tubers and tuber specific gravity

Indices	Tuber yield			Percentage of large tubers			Tuber specific gravity		
	Mean under stress	Mean in the absence of stress	Mean of the envi-ronments	Mean under stress	Mean in the absence of stress	Mean of the envi-ronments	Mean under stress	Mean in the absence of stress	Mean of the envi-roments
Index 1	0.85**	-0.49**	0.07	0.72**	-0.48**	0.16	0.48**	-0.36**	0.08
Index 2	-0.86**	0.49**	-0.08	-0.75**	0.45**	-0.20	-0.48**	0.36**	-0.08
Index 3	0.94**	-0.29*	0.30*	0.91**	-0.16	0.48**	0.89**	0.23	0.62 **
Index 4	0.86**	0.48**	0.89**	0.87**	0.69**	0.99**	0.91**	0.90**	1.00**
Index 5	0.96**	0.24	0.75**	0.95**	0.50**	0.92**	0.96**	0.83**	0.99**
Index 6	-0.85**	0.49**	-0.08	-0.72**	0.48**	-0.16	-0.48**	0.36**	-0.08
PR[1]	-0.85**	0.49**	-0.08	-0.72**	0.48**	-0.16	-0.48**	0.36**	-0.08
Geometric mean	0.86**	0.48**	0.89**	0.86**	0.70**	0.99**	0.91**	0.90**	1.00 **
Mean of the environments[2]	0.55**	0.80**	1.00**	0.79**	0.78**	1.00**	0.91 **	0.90 **	1.00**

[1] percentage of reduction in the trait; [2] arithmetic mean. ** and * significant at 1% and 5% probability by the t test, respectively

Table 3. Means for tuber yield (g plant^{-1}) of 15 clones in the presence (ME) and absence of environmental stress (MF), with the respective selection indices (SI)

Clone	ME	MF	AM[1]	GM[2]	SI 1	SI 2	SI 3	SI 4	SI 5	SI 6	PR
CBM 15-10	455	1561	1008	843	0.29	1.10	0.17	1.20	1.09	1.23	71
CBM 15-25	674	1242	958	915	0.54	0.59	0.47	1.42	1.91	0.80	46
CBM 16-15	604	1285	945	881	0.47	0.72	0.37	1.32	1.59	0.92	53
CBM 16-16	613	1381	997	920	0.44	0.77	0.35	1.43	1.75	0.97	56
CBM 16-28	237	1022	629	492	0.23	1.25	0.07	0.41	0.19	1.34	77
CBM 2-16	400	962	681	620	0.42	0.83	0.21	0.65	0.52	1.02	58
CBM 2-21	773	955	864	859	0.81	0.21	0.81	1.25	1.93	0.33	19
CBM 2-03	482	1177	829	753	0.41	0.84	0.25	0.96	0.92	1.03	59
CBM 2-06	326	1425	875	681	0.23	1.26	0.10	0.79	0.51	1.34	77
CBM 22-19	684	1342	1013	958	0.51	0.65	0.45	1.56	2.13	0.85	49
CBM 22-07	355	1292	824	677	0.27	1.14	0.13	0.78	0.55	1.26	73
CBM 24-06	725	1195	960	931	0.61	0.49	0.57	1.47	2.13	0.68	39
CBM 7-12	584	1122	853	809	0.52	0.63	0.39	1.11	1.29	0.83	48
CBM 8-11	652	1003	828	809	0.65	0.42	0.55	1.11	1.45	0.61	35
CBM 8-03	557	1382	970	877	0.40	0.85	0.29	1.30	1.45	1.04	60

[1] AM: arithmetic mean and [2] GM: geometric mean (g plant^{-1}); SI: selection index and PR: percentage of yield reduction (%)

to favorable cultivation conditions, and quite sensitive. This classification can also be realized by index 6, which had been used by Tai et al. (1994) to describe the reaction of potato genotypes to heat; the lowest value of 0.33, for CBM 2.21, indicates tolerance and the highest value of 1.34, for CBM 2-06, indicates sensibility.

Among the best criteria for selection are the geometric and arithmetic means of the environments, which also presented high correlation with the means in the environments with and without stress, principally for the trait of highest heritability, tuber specific gravity (Table 2). In the case of tuber yield, the geometric mean presented a higher correlation with the mean under stress (0.86). The arithmetic mean presented a higher correlation with the mean in the absence of stress (0.80) (Table 2). This indicates that, based on the arithmetic mean, the selection of low-performing genotypes in the environment under stress is possible. This same tendency in relation to the correlations established with the geometric and arithmetic means were found by Abebe et al. (1998) and Yadav and Bhatnagar (2001) for favorable and water stress conditions, in studies with common bean and pearl millet, respectively. In this setting, the arithmetic mean, the geometric mean or index 4 can be recommended for clone selection. It is worth mentioning that the criteria can further be used in combination, aiming at an enhanced selection safety. Selection by index 4 should be joined with the mean in the favorable environments, since it is stronger correlated with yield under stress.

For a better visualization of the results, we proposed a plot of the environment means, following the suggestion of other studies, but using indices (Nicholaides and Piha 1987, Parentoni et al. 2001, Durães et al. 2002). In the plot clone means in the favorable environment are represented on axis x and means in the stress condition on axis y (Figure 1). Two straight lines cut the axis x and y in the respective overall means of these environments, separating four quadrants, similar to the index presented by Nicholaides and Piha (1987) and Parentoni et al. (2001). The plot allows the identification of the responsive clones to improved environments and with higher mean in the unfavorable environment (quadrant I in the plot, Figure 1).

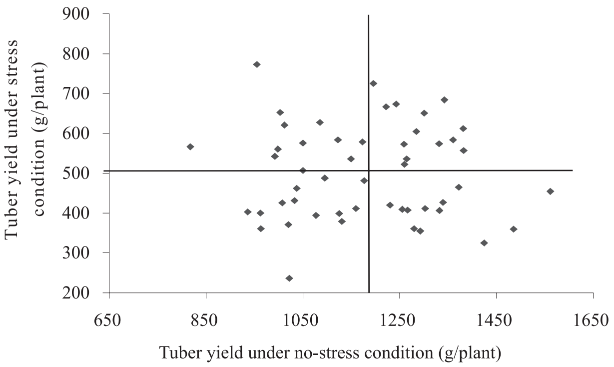

Figure 1. Relationship between average tuber yield under stress and no-stress conditions

The indices indicated as promising to support for selection are pretty simple and easy to apply in the routine of improvement programs. To underscore the importance of the selection based on the environment mean, Figure 2 shows the relation between the means of the five best clones selected based on the mean of the favorable environments (CF), in the mean under stress conditions (CE) and based on the mean of all environments (CM), for the three traits.

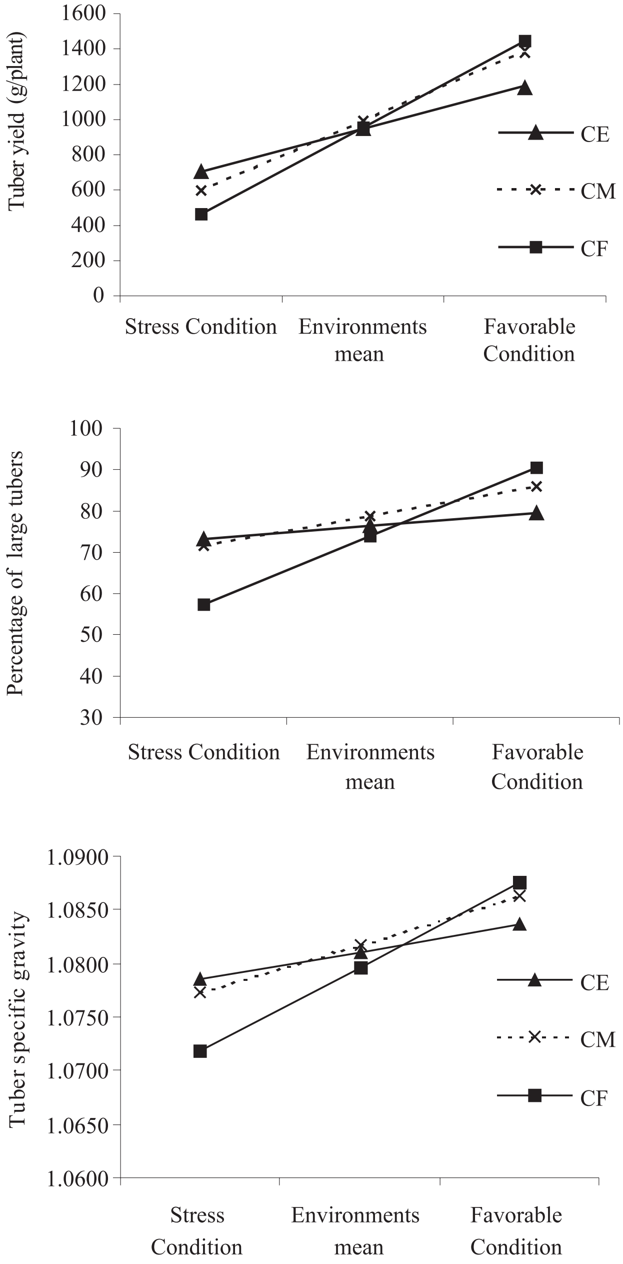

Figure 2. Performance of the five best clones selected based on the mean under stress condition (CE), on the mean of all environments (CM), and in favorable conditions (CF) for tuber yield per plant (a), percentage of large tubers (b), and tuber specific gravity (c)

The same response pattern is observed for the three traits: the mean of the best clones CF was inferior to the clone mean CE in the stressful environments.

The opposite was observed as well, where the mean of the best clones selected under stress (CE) was inferior in the favorable environment. The clones selected based on the means of the environments (CM) presented middle-rate performance in the favorable as much as the unfavorable conditions. For tuber yield, e.g., the five best clones CE were 52% more productive than CF under the stress conditions, but produced 21% less in the favorable environments. These results are in line with those generally found in improvement studies of stress conditions (Cecarelli et al. 1992, Cecarelli et al. 1998) and as demonstrated theoretically by Rosielle and Hamblin (1981).

If one aims at a broader genotype adaptation, considering the results of the indices, the clones must be selected based on the environments mean. But, if the program is directed to select genotypes recommended for conditions of high temperatures only, evaluations in the rainy summer season should be given priority. This was also indicated for barley improvement, specifically under water stress conditions (Cecarelli 1989). Though many experiments under stress conditions were not satisfactory in view of the low heritability, only the evaluation in these environments can indicate the traits for which the genotypes should present good performance. In the case of potato clone selection for heat stress, additional traits ought to be considered, such as the resistance to physiological disorders.

Table 4 displays the expected genetic progress for the traits with the selection performed by different criteria. Gains were considerably high for the traits with the truncation selection based on the mean of the environment itself. This is the case because when selection is performed for a specific environment only, the genotype x environment interaction can be capitalized on, considering that the genetic variance of the individual environments is inflated by the component of the interaction. The gains for tuber specific gravity seem low at a first glance (mean=1.2%) compared to those obtained for the other traits. However, assuming that the clone mean in an environment is 1.070, with selection and an expected gain of 1.2%, this mean would rise to 1.0828, considered ideal for tuber quality. An increase of 0.005 unit in tuber specific gravity represents about 1% in the tuber dry matter content (genotypes with values of over 20% dry matter are desirable).

The progress expected in the environment mean based on selection that is in turn based on the mean of the environments was lower than the direct progress (Table 4). This is the case because in the expressions of the mean-based gains the components of genetic variance of the joint analysis are used which are free of the component of the genotypes x environments interaction, and therefore closer to gains achieved in

Table 4. Mean expected genetic progress (%) with the selection performed under different criteria for tuber yield, percentage of large tubers and tuber specific gravity

Description	Tuber yield	Percentage of large tubers	Tuber specific gravity
Mean of the direct progress[1]	39.00	29.10	1.20
Progress in the mean with the selection in individual environments[2]	5.06	11.21	0.64
Progress in the mean with the selection based on the overall mean of the environments	6.87	22.08	0.95
Progress in the individual environments with the selection in the overall mean of the environments	15.09	19.54	0.99
Mean correlated responses[3]	3.29	13.34	0.76
Means of the efficiencies of indirect selection in relation to that practiced based on the performance in the environment itself	9.15	47.81	66.24

[1] mean of all genetic progress obtained for each environment separately - selection based on the performance in one environment (i) and progress in the same environment (i)
[2] mean of the genetic progress obtained with the selection in one environment (i) and progress in the mean of the environments
[3] mean of the indirect genetic progress - obtained in the selection in one environment (i) and progress in another environment (j)

practice. Selection in improvement programs is usually mean-based. It was further observed that gains in the mean with selection in the mean as well are higher than gains in the mean, but with selection in individual environments.

Table 4 further shows the progress expected with indirect selection for the environments. The gains were lower than those expected with selection of the environment mean and the efficiency of indirect selection in relation to selection based on the environment itself was low. Several studies show that direct is frequently more effective than indirect selection, as suggested in the theoretic study of Rosielle and Hamblin (1981). This was confirmed by numerous experiments revised by Cecarelli (1994) and also stated by Resende et al. (1997) and Atlin and Frey (1990) for stress conditions. The reason for the low efficiency of indirect selection can be explained by the low correlations, some of which even negative, observed among clone means in the different experiments for the traits (data not shown). Correlations were low, mainly for tuber yield, which varied from –0.37 to 0.48. The correlation coefficients for percentage of large tubers varied from –0.16 to 0.64 and from 0.23 to 0.68 for tuber specific gravity.

Melhoramento da batata para condições tropicais: II. Índices de seleção e eficiência de seleção indireta

RESUMO - *O objetivo deste trabalho foi estudar índices que possam contribuir para a seleção de clones de batata para condições de cultivo favoráveis ou sob estresse, procurando-se avaliar também a viabilidade da seleção indireta para tolerância ao calor. Entre os índices de seleção, a média aritmética, a média geométrica e o índice 4 são os mais indicados. O índice de susceptibilidade ou a porcentagem de redução da produção somente indicam os materiais especificamente adaptados. A seleção indireta não é indicada para tolerância ao calor, sendo ineficiente em virtude das baixas correlações entre médias de clones nos ambientes. A seleção baseada na média dos ambientes é mais indicada quando se deseja selecionar genótipos com ampla adaptação. No geral, os clones com os melhores desempenhos sob estresse ambiental e, considerados tolerantes ao calor, são especificamente adaptados, com média baixa em ambientes favoráveis. No entanto, genótipos com bom desempenho em ambas condições podem ser selecionados.*

Palavras-chave: Solanum tuberosum *L.*, tolerância ao calor, melhoramento genético.

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