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Yield Stability and Late Blight Resistance Analysis among Potato Clones Bred with Quantitative Resistance

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Abstract: Thirteen promising clones from population B3C2 potato genotypes (bred for quantitative resistance to late blight) obtained from the International Potato Center and three control cultivars were evaluated for four planting dates within two cropping seasons at Kalengyere Research Station in Southwestern Uganda in order to determine performance and yield stability. The analysis of variance of the relative area under disease progress curve (rAUDPC) revealed significant difference ($P < 0.001$) among genotype × planting date interaction, and significant difference ($P < 0.001$) among genotypes × fungicide treatments × planting date interaction. The analysis of variance (ANOVA) of yield revealed also significant difference among genotypes × planting date interaction and significant difference ($P < 0.05$) among genotypes × fungicide treatments × planting date interaction, showing the variable response of genotypes and the need for stability analysis. The additive main effects and multiplicative interactive (AMMI) statistical model showed that the most stable and high yielding genotypes were 396038.107, 396026.103 and 393280.82. The cultivars Victoria, Nakpot 5 and Cruza recorded low yields (below the average), but Nakpot 5 was generally more variable, and is therefore highly adaptable to some environments.

Key words: Potato, yield stability, late blight resistance.

1. Introduction

The program for the improvement of potato populations by increasing gene frequencies for quantitative (horizontal) resistance to late blight had been initiated by the International Potato Center (CIP) [1] since 1990. As achievements, population B1 was developed through several recombination cycles of resistance sources of *Solanum andigena*; population B2 was obtained from crosses between *S. andigena* and *S. tuberosum* sources of resistance, while population B3, the most advanced source of quantitative resistance currently available at CIP, was selected from population A and contains mostly *S. demissum*-derived horizontal resistance improved mainly in an *S. tuberosum* germplasm background [2].

Despite the fact that the improvement is made, the expression of quantitative resistance can be affected by environmental conditions [3], which makes it difficult to study the stability of that resistance across different testing or production conditions.

One way to study the stability of quantitative resistance is through the analysis of genotype × environment (G × E) interaction. G × E effects occur when two or more genotypes differ significantly in their response to changing environments [3], and can be studied temporally (two or more seasons testing at a location) or spatially (several locations) or the combination of these [4]. This study therefore, was to assess the level of late blight resistance and the yield potential of the recently introduced population B3

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cycle 2 breed for quantitative resistance under Ugandan conditions and select useful parents for a half diallel cross for further selection.

2. Materials and Methods

2.1 Planting Material

Thirteen potato genotypes namely: CIP393112.19, CIP396031.108, CIP396038.107, CIP396029.250, CIP395011.2, CIP396026.103, CIP395111.13, CIP3962241.4, CIP396004.255, CIP396031.119, CIP396244.12, CIP391046.14, CIP393280.82, obtained from CIP in 2009 were tested in field experiment. The collection is putatively carrying quantitative resistance to late blight and belongs to a population known as B3C2 [5]. In addition to horizontal resistance, population B3 has also been improved for tuber yield, dry matter content and early tuberization, bulking, quality for potato fries and chips [5]. Three local varieties were included in the experiment, namely Victoria, Cruza and Nakpot 5. Victoria was released in Uganda in 1991 as a moderately resistant variety; although it is presently one of the most susceptible cultivars in Uganda. Cruza is a popular cultivar grown widely in Rwanda, Burundi and parts of Congo Democratic Republic where it has kept its level of resistance to the disease for decades [3]. Cultivar Nakpot 5 is a recent variety release in Uganda reputed for its high levels of late blight resistance and high yields.

2.2 Source of Inoculum

The Ugandan isolates which belong to the clonal lineage US-1 of *Phytophthora infestans* are assumed to be the pathogen infecting plants in all the experiments [6].

2.3 Field Experiments

All experiments were conducted in Karengyere Research Station (2,450 m above sea level) in Southwestern Uganda representing one of the major potato growing areas of the country. The soils are volcanic (andosols) and fertile with a pH of 4.75 [7]. This is a location of consistently high disease pressure and for that reason it is used for screening of populations of potato genotypes segregated for resistance to *P. infestans*. The experiments were carried out during four planting dates which coincided with the long rains of from September 2009 to February 2010 (2009B) and short rains of from March to July 2010 (2010A).

The experimental layout was a randomized complete block design (RCBD) in a split plot arrangement, with two replications. The spray regimes (sprayed versus unsprayed) were the main plots, while potato genotypes were the sub-plots. Each sub-plot consisted of one 4 m long single row with 10 plants because of limited seeds. Inter-row spacing was 0.80 m and intra-row spacing of plants was 0.40 m. Plots were separated from each other by 1 m wide fallow areas. Hand weeding and light hilling were done between four and six weeks after plant emergence. Fertilizer (N:P:K = 17:17:17) was also applied at the rate of 120 kg/ha.

2.4 Assessment of Late Blight Resistance in the Field

Assessment of late blight severity started at the onset of the disease symptoms; disease severity rating was based on visual symptoms, using a 1-9 CIP scale where 1 is equivalent to no infection and 9 is 100% infection [8] for a total of 8-10 readings per experiment. Late scores were used to calculate areas under disease progress curves (AUDPC) which were subsequently standardized to give relative AUDPC [9]. AUDPC was calculated for individual plants using the original late blight severity data with the formula $\text{AUDPC} = \sum[(x_i + x_{i+1})/2] \times t_i$ in which x_i and x_{i+1} are severity (percentage of leaf area with symptoms) on date i and date $i + 1$, respectively, and t_i = days between date i and date $i + 1$. At harvest, data were collected on tuber number and fresh weights, which were used to compute number of tubers per plant and mean tuber weight (g); these values were used to calculate the overall yield per hectare (kg/ha).

2.5 Statistical Analysis

The disease's relative area under disease progress curve (rAUDPC) and yield data were subjected to analysis of variance (ANOVA) to test for significance of variation due to genotypes, date of planting, spray treatment and their interactions using GenStat 12th edition. To determine the effects of G × E interactions (referred as planting dates in our case) on yield, the data were subjected to additive main effects and multiplicative interaction (AMMI) analysis using GenStat discovery edition 3 [10]. The multiplicative effects of G × E interactions were assessed by principal component analysis (PCA).

The AMMI model was calculated as follows: $Y_{ge} = \mu + \alpha_g + \beta_e + \sum_n \lambda_n \gamma_{gn} \delta_{en} + \rho_{ge}$; where, Y_{ge} = observed yield of genotype g in environment e; μ = grand mean; α_g = deviation of the genotype g from the grand mean; β_e = deviation of environment e from the grand mean; λ_n = square root of the eigenvalues; γ_{gn} = PCA scores for genotypes; δ_{en} = PCA scores for environment e; n = number of PCA axes retained in the model and ρ_{ge} = the residual.

3. Results and Discussion

3.1 Late Blight Severity

Planting date effects were not significant ($P \leq 0.05$) for late blight severity during the cropping season B, but were significant ($P \leq 0.05$) in the cropping season A. The effects of potato cultivar for late blight severity were highly significant ($P \leq 0.01$) across the seasons. The interactive effects of planting date and fungicide treatment for late blight severity were highly significant ($P \leq 0.001$) across the seasons. The interactive effects of planting date and potato cultivar for late blight severity were highly significant ($P \leq 0.001$). Interactions between potato cultivar and fungicide treatment for late blight severity were highly significant ($P \leq 0.001$) across the seasons.

The interactions involving fungicide treatment, cultivar and season were highly significant ($P \leq 0.001$) for late blight severity across the seasons.

The 2009B cropping seasons had a higher disease severity than the 2010A. In this season, the most late blight resistant cultivars were 396026.103 and 393280.82 (Table 1). The most susceptible cultivar was 391046.14. When compared to Cruza, the most late blight resistant cultivars were 396026.103 and 393280.82 (Table 1). During 2010A, late blight severity had generally decreased. All the cultivars compared to Cruza were late blight resistant except 391046.14 and Victoria. The most late blight resistant were 396029.250, 395011.2, 393280.82 and 395112.19 (Table 1). The late blight moderately resistant cultivars were 395111.13, 396031.108, 396244.12, 396038.107 and 396004.255 compared to Nakpot 5 and Victoria (Table 1). The most late blight resistant cultivar when there is no protection with fungicide was 396026.103. The most susceptible cultivars were 391046.14, 395111.13 and 396031.119 compared to Victoria (Table 1).

Table 1 Mean rAUDPC of 12 genotypes and three local varieties at Kalengyere, 2009B and 2010A cropping seasons.

Season	2009B		2010A	
Genotypes	PD1	PD2	PD1	PD2
391046.14	44.8	52.4	30.0	10.1
393280.82	10.4	12.6	4.1	2.9
395011.2	27.3	16.9	5.1	2.0
395111.13	38.9	43.4	6.5	3.3
395112.19	17.6	42.8	5.6	6.0
396004.255	33.1	17.6	8.9	6.2
396026.103	10.2	5.15	14.4	8.8
396029.250	35.7	29.3	3.7	2.0
396031.108	28.8	14.9	8.4	3.9
396031.119	42.2	46.2	25.1	7.5
396038.107	30.6	19.1	11.8	4.5
396244.12	22.0	22.6	6.3	5.3
Cruza	11.3	9.7	8.3	2.3
Nakpot 5	40.6	24.6	17.9	2.1
Victoria	39.0	48.2	35.6	27.9
Mean	28.8	27.0	12.8	6.3

PD1: planting date 1 = September 3, 2009 and March 31, 2010, PD2: planting date 2 = September 30, 2009 and April 30, 2010. $LSD_{0.05}$ for genotypes 2009B = 6.0, $LSD_{0.05}$ for interaction between planting date and cultivar 2009B = 8.7, $LSD_{0.05}$ for genotypes 2010A = 2.4, $LSD_{0.05}$ for interaction between planting date and cultivar 2010A = 3.4.

3.2 Total Fresh Tuber Yield (t/ha)

Planting date effects for fresh tuber yield were significant ($P \leq 0.05$) in the cropping season B but not significant ($P \leq 0.05$) in the cropping season A. The effects of potato cultivar for fresh tuber yield were highly significant ($P \leq 0.001$) across the seasons. The interactive effects of planting date and fungicide treatment for fresh tuber yield were not significant ($P \leq 0.05$) in the cropping season B but highly significant ($P \leq 0.001$) in the cropping season A. The interactive effects of planting date and potato cultivar for fresh tuber yield were highly significant ($P \leq 0.001$) across the seasons. In unprotected plots with fungicide, fresh tuber yield (t/ha) ranged from 12.1 t/ha for Nakpot 5 to 36.7 t/ha for 396026.103 during the 2009B cropping season (Table 2). The cultivars 396026.103, 396031.108, 396038.107 and 396029.250 were the highest yielders (Table 2). In the unprotected plots, fresh tuber yield ranged from 8.3 t/ha for 396004.255 to 24.0 t/ha for 393280.82 during the 2010A cropping season (Table 2). The genotypes 393280.82, 396026.103, 396031.108, 396038.107 and 396244.12 were the highest yielders. In the both 2009B and 2010A cropping seasons, the protected plots had higher yields than the unprotected plots (Table 2). During the season 2009B, higher fresh tuber yield (t/ha) was recorded in planting date 1 than that in planting date 2 (Table 2). Fresh tuber yield ranged from 12.5 t/ha for Cruza to 41.7 t/ha for 396031.108 in planting date 1. In planting date 2, fresh tuber yields ranged from 7.5 t/ha to 37.2 t/ha for 396026.103. The highest yielders both in planting date 1 and date 2 were 396031.108, 396026.103, 396029.250, 396038.107 and 396031.119 (Table 2). During the season 2010A, higher fresh tuber yield (t/ha) was recorded in planting date1 than that in planting date 2 (Table 2). Fresh tuber yield ranged from 6.4 t/ha for 395112.19 to 25.9 t/ha for 393280.82 in planting date 1. In planting date 2, fresh tuber yields ranged from 10.2 t/ha for Nakpot 5 to 20.6 t/ha for 393280.82. The highest yielders were 393280.82, 396038.107, 395112.19 and 396026.103.

3.3 Stability and Adaptation

The performance of genotypes varied from season B to season A, from planting date 1 to planting date 2 and varied among the genotypes which suggested the presence of G × E interaction. The G × E studies are of paramount importance in the specific environments in which the genotypes are to be grown [11]. The potato genotypes evaluation were therefore subjected to G × E analysis to determine the effect of G × E interaction on the yields (t/ha) of elite potato genotypes and to identify stable and adapted genotypes for the different planting dates in Uganda.

3.4 Fresh Tuber Yield (t/ha)

The AMMI analysis for yield across environments and environment across genotypes indicated highly significant ($P < 0.001$) treatment effects (Table 3). The interactive effects due to genotype and environment

Table 2 Tuber yield (t/ha) of 13 genotypes and three cultivars at Karengyere during 2009B and 2010A seasons.

Season	2009B		2010A	
Genotypes	PD1	PD2	PD1	PD2
391046.14	28.4	16.2	16.2	16.5
393280.82	29.8	20.6	25.9	20.6
395011.2	24.4	7.5	19.8	15.0
395111.13	20.4	15.5	11.6	12.2
395112.19	36.6	18.3	6.4	20.1
396004.255	29.0	10.8	9.3	12.8
396026.103	40.1	37.2	23.3	19.6
396031.108	41.7	35.3	22.3	18.3
396031.119	30.0	22.1	20.0	13.9
396038.107	37.6	25.0	19.8	20.4
396244.12	26.1	17.9	20.7	15.6
396029.250	37.8	31.2	13.3	17.4
Cruza	12.5	20.2	19.8	13.8
Nakpot 5	22.7	14.1	18.8	10.2
Victoria	30.8	12.2	12.4	14.7
Mean	29.9	20.2	17.3	16.1

PD1: planting date 1 = September 3, 2009 and March 31, 2010, PD2: planting date 2 = September 30, 2009 and April 30, 2010. $LSD_{0.05}$ for genotypes 2009B = 5.1, $LSD_{0.05}$ for interaction between planting date and cultivar 2009B = 7.0, $LSD_{0.05}$ for genotypes 2010A = 2.3, $LSD_{0.05}$ for interaction between planting date and cultivar 2010A = 3.2.

Table 3 AMMI analysis of fresh tuber yield.

Source of variation	Df	SS	MS
Total	119	8,543	71.8
Treatments	59	7,269	123.2***
Genotypes	14	2,919	208.5***
Environments	3	2,118	705.9**
Block	4	535	133.6***
G × E	42	2,233	53.2***
IPCA 1	16	1,140	71.2***
IPCA 2	14	779	55.7***
Residuals	12	314	26.2
Error	56	739	13.2

***significant at $P < 0.001$, **significant at $P < 0.01$, *significant at $P < 0.1$, ns = no significance, Df = degree of freedom, SS = sum of squares, MS = mean squares.

were also highly significant ($P < 0.001$) for yield. The genotype, environment and G × E interaction effects accounted for 40.2%, 29.1% and 30.7% of the treatment sums of squares, respectively. The genotypes main effects and the effects due to interaction between genotypes and environments were much larger than the effects due to environments

The analysis of the biplot revealed that the test clones 391046.14, 39511.2, 395111.13, 396031.119, 396038.107, Victoria and 396031.108 had negligible interaction with the environments. The season B, planting date 2 no spray (S1D2N) and season A, planting date 2 no spray (S2D2N) had negligible interaction with the genotypes (Fig. 1). Therefore, these genotypes and environments were considered stable, implying that the six genotypes can give high yields in any of these environments, while the respective environment can support the growth of any of the genotypes studied. The clones 391046.14, 39511.2 and 395111.13 were the most stable but had low yields (Fig. 1). Generally the season B, planting date 2 no spray (S1D2N) and season A, planting date 2 no spray (S2D2N) were the most stable environments, although they had low yields (Fig. 1). Test genotypes 396038.107 and 396031.108 were also the most stable and had higher yield than the clones 391046.14, 39511.2 and 395111.13. The clones 396004.255, 395112.19, 396029.250 and 396026.103 were the least stable and had high positive interaction

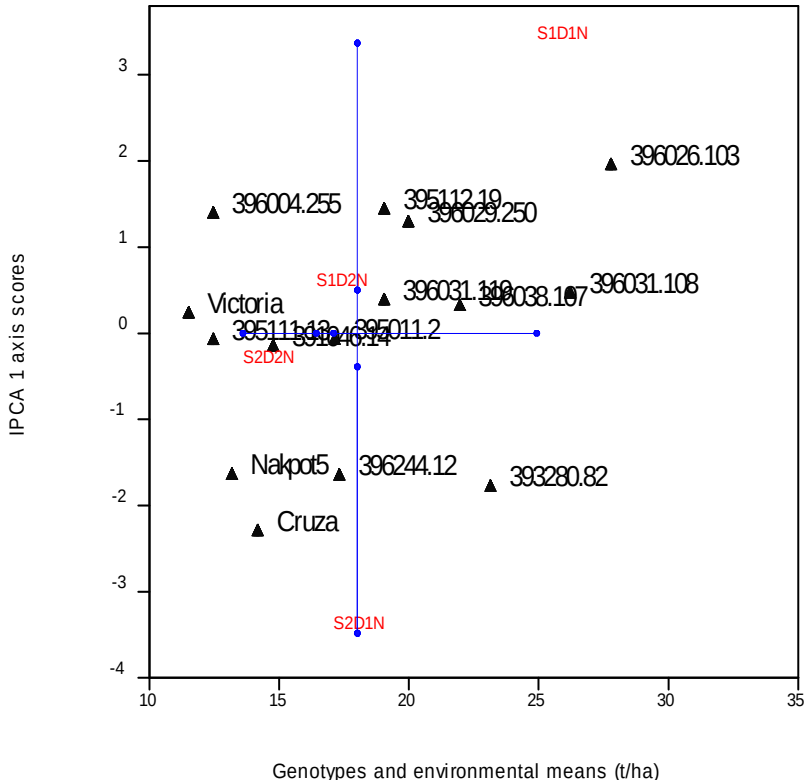

Fig. 1 Plot of mean tuber yield and AMMI interaction with (IPCA 1) scores for 12 potato genotypes evaluated in four planting dates within two seasons.

and high yields but likely not to be interactive with any specific environment (Fig. 1).

Similarly, the genotypes Nakpot 5, Cruza, 396244.12 and 393280.82 were the least stable and had high negative interaction but likely not to be interactive with any specific environment. These genotypes had low yields except the clone 393280.82 which had high yield. The environments season A, planting date one, no spray and season B, planting date one, no spray were the most unstable (Fig. 1).

The average tuber yield of potato clones from 15.0 t/ha to 30.0 t/ha are plotted on the x-axis, while the principal component analysis scores (IPCA 1) are plotted from -4.0 to +3.0 on the y-axis. The variables along the x-axis reflect differences in the main effects, and the values along the y-axis show differences in the interaction effects. The genotypes to the right side of the mid-point are classified as high yield potential, and those to the left side as low yield potential. The environments are represented by season B, planting date one, no spray (S1D1N), season B, planting date two, no spray (S1D2N), season A, planting date one, no spray (S2D1N), season A, planting date two, no spray (S2D2N).

The selection of high yielding genotypes with stable resistance to late blight and wide adaptation is a principal goal of potato breeding to late blight resistance. Genotypes with high levels of resistance to late blight are a useful tool in managing this disease particularly for poor farmers. In this chapter, 15 genotypes representing a wide range of late blight resistance were grown in two seasons with two planting dates in each season. There were highly significant ($P \leq 0.001$) interactive effects between planting date and potato cultivar, potato cultivar and fungicide treatment, and among fungicide treatment, cultivar and season for late blight severity indicating significant different responses of the genotypes to varying environments in which they were grown. Results indicated that the genotypes 396026.103, 393280.82 and Cruza were the most resistant to late blight across planting dates. These genotypes were also the most resistant to late blight in the unprotected plots across the seasons. The genotypes 391046.14 and Victoria were the most susceptible across cropping seasons. However, late blight was more severe in the cropping of season 2009B for most of cultivars due to more conducive weather for disease development.

Differences in severity levels to LB in the evaluated genotypes may be explained by genetic factors and the differences in weather conditions. Population B3 contains genotypes bred with quantitative resistance to late blight [1]. Low disease severity levels in these genotypes indicate that their resistance is horizontal and therefore may reduce the likelihood of emergence of more aggressive strains of *P. infestans* [12]. The proportion of environment and genotype main effects for late blight severity were much larger than G × E interaction effects. This is an indication that the cultivars responses varied from one environment to another suggesting that the emphasis should rely more on suitability of the environment and late blight management to decrease late blight severity rather than to rely on the genotypic differences alone.

Analysis of variance did not show interaction between genotypes and fungicide treatment for yield. The observed disease severity therefore among cultivars was not enough to affect total fresh tuber yield. This implies most of these cultivars can be grown with little or no fungicide. Instead, it is the genotype and planting date main effects that significantly affected total fresh yield. In general, the tested genotypes showed potential for very high yields. During the 2009B cropping season, the highest yielders both in planting date 1 and date 2 were the genotypes 396031.108, 396026.103, 396029.250, 396038.107, 395112.19, 393280.82 and 396031.119 with a fresh tuber yield above 18.0 t/ha. During the 2010A season, the highest yielders both in planting date 1 and date 2 were the cultivars 393280.82, 396026.103, 396031.108 and 396038.107 with a fresh

tuber yield above 18.0 t/ha. The differences in yield were first attributed to their tolerance level to late blight and secondly to environmental conditions. During 2009B cropping season, there was heavy and more frequent rain fall than in 2010A cropping season as shown by the weather data, which favored high yields on most of the genotypes in 2009B cropping season. The average yields of the test clones were promising because they were higher than yields of the checks.

Variation in yield was detected among potato cultivars across environments. The interactions involving fungicide treatment, cultivar and season for fresh tuber yield were significant ($P \leq 0.05$). This indicates that the main effects of cultivars alone were not sufficient to explain the observed yields without considering environmental effects. The environment and G × E interactions had greater influences on yield than cultivars. Previous research on yield of potato cultivars showed similar results on G × E interaction effects [13]. The analysis of the biplot revealed that the test cultivars 391046.14, 39511.2, 395111.13, 396031.119, 396038.107, Victoria and 396031.108 had little interaction with the environments; therefore they were the most stable on fresh tuber yield. The second planting of the cropping season 2009B (S1D2) and the second planting of the cropping season 2010A (S2D2) displayed high interaction with these cultivars, therefore they were considered stable. These six cultivars can therefore give high yields in any of these environments. The cultivars 396004.255, 395112.19, 396029.250 and 396026.103 were the least stable.

Although most of the cultivars were stable, AMMI and the biplot identified two cultivars 396026.103 and 393280.82 with high yields, but with no interaction to any specific environment, implying that they can grow well in any of the tested environments with positive interaction. The cultivars main effects and the effects due to interaction between genotypes and environments were much larger than the environment effects, implying that high yields could be obtained by locating the genotypes in their well adapted environments. Earlier G × E studies suggested that the effects due to interaction between genotypes and environment become larger than due to genotypes main effects, and attention should be paid on crop management and suitability of the cultivars in a given environment to attain higher yields rather than the yield differences alone among the genotypes [2, 14]. However, the two studies used potato cultivars from population A which have a different late blight genetic background.

The AMMI model was successfully used to investigate the G × E interaction and stability of fresh tuber yields of the potato population B3. There is an indication that population B3 materials were very sensitive to variations in environments as most of them were unstable, thus lowering their possible adaptability and stability to varying growing conditions. Test cultivars 391046.14, 39511.2, 395111.13, 396031.119, 396038.107, Victoria and 396031.108 had negligible interaction with the environments, therefore, they are the most stable for fresh tuber yield with good yield across all the environments. This study is significant in genotype development, because most of the genotypes have been proved to have very good yields at a site reputed for high LB severity. In conclusion, the proportion of environmental variance and the G × E interaction were greater than genotypic variance indicating that the tested cultivars were closely related but responded differently to the differences in environments.

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