Evaluation of Genetic Resources in a Potato Breeding Program for Chip Quality

Roberto Ruiz de Arcaute 1,2,3,*, Ana Carrasco 2,4, Felisa Ortega 2, Marta Rodriguez-Quijano 5 and José M. Carrillo 5

1 NEIKER—Basque Institute for Agricultural Research and Development, Basque Research and Technology Alliance (BRTA), Arkaute Agrifood Campus, E-01192 Arkaute, Spain
2 Formerly in APPACALE SA—Aggregation of Seed Potato Producers of Castilla and León SA, C/Valle de Mena 13, E-09001 Burgos, Spain; acarrasco@udapa.com (A.C.); feli_ortega@yahoo.es (F.O.)
3 Biotechnology and Genetic Resources of Plants and Associated Microorganisms, School of Agricultural Engineering, Universidad Politécnica de Madrid, Avenida Puerta de Hierro 2, E-28040 Madrid, Spain
4 UDAPA S. Coop. Union of Alava Potato Growers Cooperative, Paduleta 1, E-01015 Vitoria-Gasteiz, Spain
5 Department of Biotechnology and Plant Biology, School of Agricultural Engineering, Universidad Politécnica de Madrid, Avenida Puerta de Hierro 2, E-28040 Madrid, Spain; martaruruquiaga@upm.es (M.R.-Q.); josem.carrillo@upm.es (J.M.C.)
* Correspondence: ruizdearcaute@neiker.eus; Tel.: +34-608963505

Abstract: The objective of this study was to assess the ability of experimental advanced breeding clones as parental genotypes to transmit agronomic and quality traits to their progenies in breeding programs. A half diallel set of crosses (excluding reciprocals) with six parents was assayed in field trials for three years; four of the parents were Solanum tuberosum subsp. tuberosum cultivars, and two of them were advanced breeding clones that included genes from S. tuberosum subsp. andigenum with immunity to PVY virus and good agronomic performance. However, no information was available about the behavior of these clones as parental materials for quality traits, such as potato chip quality. The diallel mating design allowed us to discover their ability to transmit agronomic and quality traits to their offspring. Significant effects on general combining ability and specific combining ability were found for plant maturity, only general combining ability effects for specific gravity were found, and interactions of both general combining ability and specific combining ability with the environment for the chip color trait were found. However, no genetic effects were detected for yield. Where general combining ability significant effects were found, additive genetic effects are predominant; thus, so for those traits, it would be possible to use these genotypes as parents to obtain improved progenies. Such abilities were not found in the advanced breeding clones.

Keywords: germplasm; Solanum tuberosum subsp. andigenum; breeding for quality; progeny testing

1. Introduction

Modern improved potato cultivars in the northern hemisphere belong to the autotetraploid species Solanum tuberosum subsp. tuberosum (=Chilotanum group, 2n = 4x = 48). Potato breeding of the tetraploid Chilotanum group in regions with temperate long-day summers has always been constrained by the narrow genetic base of this subspecies [1]. However, today it is unclear whether European cultivated potatoes evolved differentially from a common Andean origin for the two subspecies of S. tuberosum (S. t. andigenum and S. t. tuberosum) or S. t. tuberosum has an independent Chilean origin [2], but the Solanum gene pools are wide and flexible, and they are relatively amenable to be used in breeding [3]. The poor adaptation to the European long-day photoperiod conditions in a first stage and the blight epidemics in the 19th century are likely to be some of the reasons for this [2,4,5]. Genetic variability among 20th century cultivars was low, as evidenced by low estimates of genotypic variance in tuber yield trials, and new varieties have not made major
breakthroughs on yield [2]. Genetic variation is desirable because it has a buffer effect in face of environmental stresses, disease pressure, and pest damages. On the other hand, a positive relation between genetic diversity and tuber yield has been found, since genetic divergence among parents can promote heterosis [6]. It is also necessary to improve some important traits in varieties focused on a commercial objective, such as plant maturity and quality traits. A correlation between late plant maturity and higher tuber yield has been reported [7], but genotypes with early tuber set and faster tuber bulking can better escape diseases severity [8], so earliness and good yield might be needed, for instance, in warm environments. Regarding quality, potatoes intended for industrial processing are defined by several quality traits, with the most important being the specific gravity of the tubers (correlated with dry matter and starch content), and the fry color [3]. Higher values of dry matter imply greater yield in the chips production, since practically all the water contained in the tubers is lost during processing. Regarding chip color, the chips should be light or very light yellow; the dark brown chips are not commercially attractive, and they tend to have a certain bitter taste because of the bitter products produced by the non-enzymatic browning (Maillard’s reaction) in the frying process. Breeding potatoes for quality traits requires a continuous flow of new genes and allelic diversity into the S. tuberosum gene pool [9].

Potato production is estimated to be 359 million tons per year all over the world, cropped on 16.5 million hectares [10], so it stands as the third most important food-source crop after wheat and rice, and the most important non-cereal food crop [11]. In the European Union, a significant part of the potato production is processed into French fries (chips in UK), chips (crisps in UK), and starch, as 9.40 million tons of processed products are sold in the EU, from which 2.27 million tons (about 24% of the total sold product) were processed in 2019 as chips [12].

Because of the importance of processed potato products, one of the objectives of any potato breeding program—as that of the company Appacale (Burgos, Spain)—is the development of good new processing varieties. However, obtaining new potato varieties is a challenging task, due to the genetic complexity of the potato as an autotetraploid species and the high heterozygosity of the species [2,13,14].

The conventional breeding approach by phenotypic selection is not very efficient, as ten to twelve years are needed to obtain a new variety if no other tools are put into practice [1,15,16]. The bottleneck of the narrow genetic base of the breeding materials, together with the absence of resistance to the harmful potato virus Y (PVY) in most of the parental lines used, led us to the opening of two new breeding lines. The first line incorporated into the breeding program our own advanced clones, which originated in crosses among parents with a genetic base of S. t. andigenum type (=Andigenum group, $2n = 4x = 48$) obtained at the International Potato Center (CIP Lima, Peru), with immunity genes to PVY and a certain adaptation to tuberize in a long-day photoperiod on the one hand, and commercial varieties with a S. t. tuberosum genetic base on the other. Advanced clones were selected for their performance and traits after several years of field trials [13,17–19]. The second line opened a breeding line at the diploid level ($2n = 2x = 24$) and incorporated different wild species with traits of resistance to cyst nematodes, PVY, and other viruses, as well as high dry matter content [20,21].

Progeny testing has demonstrated genetic gains in potato quantitative traits’ breeding, as intense early visual selection has proven to be ineffective. Mating designs allow us to obtain estimates of the performance of parental lines by calculating their combining abilities, namely general combining ability (GCA) and specific combining ability (SCA), as well as estimates of the heritability of different traits [22,23]. They provide the most valuable information for the breeding program at the same time that commercial varieties are generated. Among the different types of mating designs that have been described and contrasted [24], the diallel mating design is the most performant to estimate the combining ability of the parents for the transmission of favorable traits [23,24].
The heritability of any quantitative trait is another way to express the degree to which offspring can be expected to resemble their parents for a specific trait. This heritability can refer to the proportion of total genetic variation—including not only additive but also the effects due to dominance and epistasis—to the phenotypic variation, being then named broad-sense heritability ($H^2$), or to the narrow-sense heritability ($h^2$), which indicates the part of the phenotypic variance that is explained by the additive genetic variance. The advantage when breeding clonally propagated species such as potato is that, though narrow-sense heritability better explains the additive genetic effects, the broad-sense heritability is more useful because both additive and non-additive gene actions can be transferred and fixed from parents to offspring as early as in the first F$_1$ generation [24].

From 2000 to 2004, an experimental breeding process based on a partial diallel mating design was carried out in Appacale, incorporating unconventional germplasm derived from a pre-breeding stage of the program itself, which included parentals with interesting agronomic and disease-resistance traits—such as immunity to potato virus PVY—with a genetic background of the S. t. andigenum subspecies. The objective was to evaluate the ability of the parents to transmit their agronomic and quality characters to their progenies. This information on the parents would allow for the acceleration of the breeding process, improving the agronomic and quality traits of the bred progenies to get new and better varieties faster.

2. Materials and Methods

2.1. Plant Materials, Crosses, and Mating Design

An incomplete partial diallel set of crosses (Griffing Method 4, with no reciprocals F$_1$s nor self-crosses of parents, odel 1 because all factor effects were considered fixed) [25] was made with 6 parents, four of them being commercial varieties and the other two advanced breeding clones from S. t. andigenum germplasm with PVY immunity that were selected [19] for agronomic conditions and processing quality. The materials included in the trial along with their parentage and main quality features are listed in Table 1 [26,27].

Table 1. Parents used in crosses.

| ID | Genotype  | Parentage                   | Status         | Origin         | Quality Traits |
|----|-----------|-----------------------------|----------------|----------------|----------------|
| 1  | Caesar    | Monalisa × Rop B 1178       | Cultivar       | The Netherlands| Boiling, fries |
| 2  | Hertha    | Dijkhuis 61-133-3 × Konst 62-374 | Cultivar      | The Netherlands| Chips          |
| 3  | Tomensa   | ST 155 × Taiga             | Cultivar       | Germany        | Chips          |
| 4  | Atlantic  | Waseon × Lenape            | Cultivar       | USA            | Chips          |
| 5  | 95P87-4   | Frisia × V-2              | Breeding line  | Spain          | Boiling, fries |
| 6  | 95P17-3   | Iroise × V-2              | Breeding line  | Spain          | Boiling, fries |

Advanced clones had one commercial variety as their mother parent and the advanced breeding clone V-2 from CIP as their male parent, with the latter one having PVY immunity by R$_y$adg gene from S. t. andigenum in its pedigree [19]. “Iroise” is a variety bred in France (Fédération des Syndicats Bretons, 1982) for the fresh market, with “Katahdin” and F70 24.1, a breeding advanced French clone, in its pedigree [27,28]. “Frisia” is a multi-purpose Dutch bred (ZPC 1988) with resistance to the Ro1 pathotype of the potato cyst-nematode Globodera rostochiensis from (VT$^n$)²62-33-3, a clone that includes S. vernei and S. t. tuberosum in its pedigree [28,29].

A total of 15 combinations were made, from which one cross failed to produce seeds, so 14 progenies were successfully obtained (Table 2). The mean values of the two parents of the failed cross in the same field trials were used as means of that progeny in the data analysis.
Table 2. Progenies obtained from crosses.

|       | Caesar | Hertha | Tomensa | Atlantic | 95P87-4 | 95P17-3 |
|-------|--------|--------|---------|----------|---------|---------|
| Caesar| X      | 2001D12| 2001D4  | 2001D16  | 2001D1  | 2001D26 |
| Hertha| X      | 2001D5 | 2001D3  | 2001D14  | 2001D11 | 2001D11 |
| Tomensa| X     | 2001D13| 2001D25 | 2001D24  | 2001D19 | 2001D19 |
| Atlantic|       | 2001D23|         | 2001D23  | 2001D19 | 2001D19 |
| 95P87-4|       |        | 2001D25 | 2001D25  | 2001D24 | 2001D24 |
| 95P17-3|       |        |         | 2001D25  | 2001D24 | 2001D24 |

2.2. Clonal Material and Experimental Fields

About 120 seeds obtained from each cross were germinated in trays. Each plantlet raised was transplanted to an individual pot, and grouped families were grown in a screenhouse at the beginning of the experiment (year 0). At harvest, 4 to 6 tubers from each pot were collected and conserved over the winter in a cold chamber.

First-year tubers of all the progenies obtained were planted in the field, in the seed potato production area of Valdelucio (42° 43' 46" N, 4° 5' 9" W) in the North of the Burgos province according to a randomized complete block design (RCB) with 2 replications. The families were identified in each block, and individual plants within each family were separated 0.75 m along in rows 0.75 m apart, as well. The unit plot consisted of a family in two parallel rows, with individual data being collected from each clone. At the time of harvest, only those clones that presented non-commercial characteristics (very late maturity and very heterogeneous tuber sizes or shapes) were discarded, with the rest being individually collected and kept as seed tubers until the next season. A total number of 922 first year clones were selected from all families to be assayed in the following years (Table 3).

Table 3. Number of individuals collected in each environment.

| ID | Cross | Parent | Parent | BU02 | BU03 | BU04 | PA04 |
|----|-------|--------|--------|------|------|------|------|
| 12 | Caesar| Hertha | 89     | 48   | 53   | 20   |
| 13 | Caesar| Tomensa| 62     | 54   | 50   | 20   |
| 14 | Caesar| Atlantic| 46     | 19   | 18   | 10   |
| 15 | Caesar| 95P87-4| 76     | 60   | 46   | 5    |
| 16 | Caesar| 95P17-3| -      | -    | 9    | 4    |
| 23 | Hertha| Tomensa| 71     | 64   | 58   | 18   |
| 24 | Hertha| Atlantic| 78     | 61   | 52   | 20   |
| 25 | Hertha| 95P87-4| 68     | 54   | 41   | 18   |
| 26 | Hertha| 95P17-3| 65     | 58   | 52   | 20   |
| 34 | Tomensa| Atlantic| 67     | 55   | 53   | 19   |
| 35 | Tomensa| 95P87-4| 74     | 56   | 51   | 20   |
| 36 | Tomensa| 95P17-3| 98     | 84   | 77   | 28   |
| 45 | Atlantic| 95P87-4| 63     | 46   | 38   | 21   |
| 46 | Atlantic| 95P17-3| 65     | 53   | 53   | 20   |
| 56 | 95P87-4| 95P17-3| -      | -    | -    | -    |
| Totals|       |       | 922    | 712  | 651  | 243  |

BU02, Valdelucio 2002; BU03, Villagonzalo-Arenas 2003; BU04, Quintanadueñas 2004; PA04, Magaz de Pisuerga 2004.

Second-year tubers were planted in the ware potato production area of Villagonzalo-Arenas in Burgos province (42°22’38” N, 3°44’20” W), also in an RCB design with two replications, similar to the previous year (BU03 site).

In the third-year, tubers of all families were sown in two different ware potato production areas of Quintanadueñas (42°22’55” N, 3°43’54” W) in the Burgos province (BU04 site), and Magaz de Pisuerga (41°57’16” N, 4°29’10” W in the Palencia province (PA04 site). Similar to the previous years, trials were arranged in a RCB design with two replications. In all the experimental fields, the crop was fertilized according to local use and irrigated when
needed. Parent material was also planted in every trial to be used as checks for maturity and quality.

The average monthly maximum and minimum temperatures, as well as the monthly average temperature from official data at 3 weather stations of the Spanish Meteorological Agency (AEMET) near each location, are shown in Table 4.

Table 4. Means of monthly maximum and minimum temperatures and monthly average temperatures for each location.

| Month | BU03  | BU04  | PA04  | BU03  | BU04  | PA04  | BU03  | BU04  | PA04  |
|-------|-------|-------|-------|-------|-------|-------|-------|-------|-------|
| Apr   | 15.8  | 13.7  | 13.8  | 4.6   | 2.3   | 1.9   | 10.2  | 8.0   | 7.9   |
| May   | 20.8  | 18.5  | 18.0  | 5.7   | 5.3   | 6.2   | 13.3  | 11.9  | 12.1  |
| Jun   | 29.2  | 26.7  | 27.4  | 12.9  | 10.7  | 12.0  | 21.0  | 18.7  | 19.7  |
| Jul   | 29.7  | 28.5  | 27.4  | 12.3  | 11.0  | 11.6  | 21.0  | 19.8  | 19.5  |
| Aug   | 32.3  | 27.4  | 25.6  | 14.4  | 11.8  | 12.0  | 23.4  | 19.7  | 18.8  |
| Sep   | 24.7  | 24.8  | 23.8  | 10.2  | 9.6   | 10.8  | 17.4  | 17.3  | 17.3  |
| Oct   | 15.4  | 18.1  | 16.6  | 6.0   | 7.5   | 7.1   | 10.7  | 12.8  | 11.9  |

BU03, Villagonzalo-Arenas 2003; BU04, Quintanadueñas 2004; PA04, Magaz de Pisuerga 2004.

Visual assessments of each individual were made in the ware area trials for several traits, e.g., vegetative development, haulm cover, growth habit, and vine aspect on a 1 (poor) to 9 (excellent) scale. Plant maturity cycle (PM) was scored by comparison with control varieties on a 1 (very late) to 9 (very early) scale. At harvest, visual tuber aspect was scored on a 1 (poor) to 9 (excellent) scale, and data of total weight of tubers per individual (TW) in grams (precision +/- 0.01 g) were collected. After that, the clones were stored refrigerated in a cold chamber at 8 °C prior to submit them to the quality analysis.

2.3. Quality Analysis

Tubers of clones from the second- and third-year trials (ware potato production areas) were submitted to a quality analysis. Two traits were analyzed: the dry matter, measured as specific gravity; and chip color after frying.

Specific gravity (SG) was evaluated by calculating the difference between air weight and underwater weight for tubers, using the formula SG = (weight in air)/(weight in air−weight in water). The standard procedure involves washing the whole production of tubers of every plant at room temperature, drying them carefully, and weighing them in air and under water at room temperature [30]. Weight data were obtained in a precision hydrostatic balance that could accept any weight up to 6000 g (weight error +/- 0.01 g).

For chip color (CC), the two most representative tubers of every individual were selected and cut in two halves along. Then two longitudinal slices, 0.9 mm thick, were obtained from every tuber, using a machine with a rotary circular disc from navel to apex, in order to imitate the industrial method as far as possible, and resulting in four chips per individual. The chips were then fried for 3 min in sunflower oil heated to 180 °C in an electric fryer. Under these conditions, the oil temperature dropped to 155–160 °C, depending on the slice size, with little variation during the first minute, and then rose slowly toward the end of the process, finishing at around 170 °C [31]. Chip-color values were obtained by comparison with standard color charts [32] in which the color of the sample is rated on a 1 (very dark) to 9 (very clear) scale. The data used in the analysis were the average of the four chip-color values of each individual. Appropriate commercial scores for chip color are 7 to 9, while scores below 5 cannot be marketed [32].

2.4. Data Analysis

2.4.1. Analysis of Variance

Individual data on plant maturity (PM), weight of tubers per individual (TW), specific gravity (SG), and chip color (CC) were submitted to an analysis of homoscedasticity prior to
the analysis of variance by means of a Bartlett’s test. Then the mean values of these traits for the progenies were submitted to an analysis of variance, using the GLM procedure of the SAS/STAT 9.1 statistical system [33]. Data were analyzed by following the ANOVA model for different factors according to the Griffing model [25,34], including the environment factor and the interactions between crosses and environments effects. In this model, each combination of location by year was considered a level of the fixed environment factor (site). The SAS program Dhiallel-SAS05 [35,36] was used to analyze the variance effects of environments, replications, crosses, GCA, and SCA and their interactions. This program was used also to obtain the GCA and SCA estimates for every parent and cross, assuming a fixed model. If significant differences were found, the means of progenies were compared through a Waller–Duncan test with SAS.

2.4.2. Estimation of General and Specific Combining Abilities

The general linear model to analyze multi-environment data for Method 4, is based on the models of Griffing and Cockerham [37,38], where the value observed from each experimental unit $Y_{ijklc}$ (i and j, parents; k, replication; l, location; and c, sample) is the sum of the population mean, $\mu$; the environment effect, $\alpha_e$; the replication within environment effect, $b_{ik}$; the $F_1$ hybrid effect, $\theta_{ij}$; the interaction between $F_1$ hybrids and environments $(a\theta)_{ijl}$; and the residual effect, $e_{ijklc}$. It is expressed as follows:

$$Y_{ijklc} = \mu + \alpha_i + b_{ik} + \theta_{ij} + (a\theta)_{ijl} + e_{ijklc}$$

where $\theta_{ij}$ is the sum of the general combining ability (GCA) effect for the $i$th parent $g_i$, the GCA effect for the $j$th parent $g_j$, and the specific combining ability (SCA) effect for the $ij$th $F_1$ hybrid:

$$\theta_{ij} = g_i + g_j + s_{ij}$$

and where $(a\theta)_{ijl}$ is the sum of the interaction between GCA effect for the $i$th parent and environments $(ag)_{ijl}$, the interaction between GCA effect for $j$th parent and the environments $(ag)_{jl}$, and the interaction between SCA effect for the $ij$th $F_1$ hybrid and environments $(as)_{ijl}$:

$$(a\theta)_{ijl} = (ag)_{ij} + (ag)_{jl} + (as)_{ijl}$$

Table 5 shows the mean squares, the expected mean squares, and the F test model for each factor.

| Variation Sources | DF  | MS   | Expected Mean Squares | F Test |
|-------------------|-----|------|-----------------------|--------|
| ENV               | $e-1$ | MS5  |                        |        |
| REP(ENV)          | $e \ (r-1)$ | MS4  |                        |        |
| $F_1$ CROSSSES (G) | $(n \ (n-1) / 2) - 1$ | MS3  | $\sigma^2 + re^2_{H2Env} + re[1/(v-1)]\Sigma h^2_i$ |        |
| GCA               | $n-1$ | MS3.1 | $\sigma^2 + 2re_{GCA*Env} + 2re[(n-2)/(n-1)]\Sigma g^2_i$ | MS3.1/MS2.1 |
| SCA               | $(n \ (n-3) / 2)$ | MS3.2 | $\sigma^2 + 2re_{SCA*Env} + 2re[2/n(n-3)]\Sigma \Sigma h^2_i \ (i < j)$ | MS3.2/MS2.2 |
| $G * Env$         | $(c-1) \ (e-1)$ | MS2  | $\sigma^2 + re^2_{H2Env}$ | MS2/MS1 |
| GCA * Env         | $(n-1) \ (e-1)$ | MS2.1 | $\sigma^2 + 2r(n-2)\sigma^2_{GCA*Env}$ | MS2.1/MS1 |
| SCA * Env         | $(n \ (n-3)/2) \ (e-1)$ | MS2.2 | $\sigma^2 + 2r\sigma^2_{SCA*Env}$ | MS2.2/MS1 |
| Error             | $e \ (r-1)$ | MS1  | $\sigma^2$ |        |

DF = degrees of freedom; MS = mean squares; $e =$ environments; $r =$ replications; $n =$ parents; $c = n \ (n-1)/2$.

The raw data for the analysis of variance were the average values of the plot for each trait, obtained as the mean of the individual data collected for each of the progeny individuals in that plot.

Genotypes and sites were considered fixed factors (Griffing Model I). Since only half of total crosses were made (no reciprocals), the modified analysis of Griffing Method 4
was used [37]. The variance of hybrids factor was partitioned into the variation source due to the genetic effects of parents (GCA) and the effects of crosses themselves involving additive, dominance, and interaction effects (SCA). The interactions of crosses, GCA, and SCA with environments were similarly derived.

To test mean squares for hybrids and GCA and SCA effects, the interaction between environments and the corresponding component in the fixed effects model is used as the error term [36]. The combined ANOVA for the trials with the mean squares and appropriate F test for each source of variation is outlined in Table 5.

General predicted ratios (GPRs) were also calculated to estimate the relative importance of additive and non-additive gene action in the expression of traits, using a GPR as a ratio between the mean squares of GCA and of SCA [39]:

\[
GPR = \frac{2 \text{MS}_{\text{GCA}}}{\text{MS}_{\text{GCA}} + \text{MS}_{\text{SCA}}}
\]

A GPR above 0.5 means that GCA is more important than SCA in the inheritance of character.

2.4.3. Broad-Sense Heritability

The broad-sense heritability, defined as the proportion of phenotypic variation due to the genetically caused variation [24], was estimated for the evaluated traits from progeny means as the ratio between genetic variance and phenotypic variance expressed as the variances of GCA and SCA and their interactions with environments [40]:

\[
H^2 = \frac{V_G}{V_P} \approx \frac{2\sigma^2_{GCA} + \sigma^2_{SCA}}{2\sigma^2_{SCA} + \sigma^2_{GCA} + 2\sigma^2_{GCA \times \text{Env}} + 2\sigma^2_{SCA \times \text{Env}} + \sum_{i=1}^{n} \sigma^2_{e} / n}
\]

where \(\sigma^2_{GCA}\) is the general combining ability variance, \(\sigma^2_{SCA}\) is the specific combining ability variance, \(\sigma^2_{GCA \times \text{Env}}\) and \(\sigma^2_{SCA \times \text{Env}}\) are their interactions with environment variances, \(\sigma^2_{e}\) is the error variance, and \(n\) the number of environments. The upper and lower confidence limits were calculated from mean squares, following the procedure described by Knapp [41].

3. Results
3.1. Analysis of Variance

Bartlett’s analysis of the residuals indicated the homoscedasticity of the data set for all the traits. The mean squares and significant tests among genotypes show that CC was affected by a slightly significant genotype × site interaction (\(F(28,42) = 2.16, p < 0.05\)), while the other traits, such as PM, TW, and SG, were not significant for the G × E interaction (Table 6).

Table 6. Mean squares and significant tests for agronomic and quality traits among 6 parents and 15 F1 progenies evaluated in three environments.

| Variation Sources | DF | PM       | TW   | SG       | CC       |
|-------------------|----|----------|------|----------|----------|
| Site              | 2  | 22.43 ** | 3924766 ** | 0.00312 * | 14.85 ** |
| Rep (Site)        | 3  | 1.04 ns  | 30816 ns | 0.00011 * | 0.32 ns  |
| Genotype (G)      | 14 | 3.66 *** | 49745 ns | 0.00014 ** | 0.67 ns  |
| Genotype × Site (G × E) | 28 | 0.72 ns  | 59500 ns | 0.00004 ns | 0.62 *   |
| Error             | 42 | 0.46     | 46182 | 0.00004  | 0.29     |
| R^2               |    | 0.86     | 0.84  | 0.86     | 0.82     |

DF, degrees of freedom; PM, plant maturity; TW, tuber weight; SG, specific gravity; CC, chip color; *, **, and *** significant at \(p \leq 0.05\), \(p \leq 0.01\), and \(p \leq 0.001\), respectively; ns not significant.

The ANOVA shows that the main factor site did have a statistically significant effect on all the analyzed traits, as can be expected for a polyploid species strongly affected by environmental conditions (Table 6).
The analysis of the effect of the main factor genotype on the agronomic traits showed that it was significant for PM, for which the analysis showed that genotype did have a highly significant effect (F (14,28) = 5.16, p < 0.001). Nevertheless, the analysis reveals that the genotype did not have a significant effect on TW.

For quality traits the analysis of the effect of genotype shows different behavior depending on each trait. On SG the analysis showed that genotype did have a significant effect (F (14,28) = 3.21, p < 0.01). Otherwise, for CC the analysis detected a significant interaction between the effects of genotype and site (F (28,42) = 2.16, p = 0.011), but the main effect analysis showed that genotype did not have a significant effect on CC.

Genotype performance, then, did not vary between sites for all traits except chip color, and significantly influenced the vegetative cycle and the dry matter content of the progenies, but it did not affect the yield per plant. Regarding the chip color, the effect of the genotypes was significantly influenced by the location of the crop, indicating that the environmental factor had more weight for this trait than the genetic factor in this group of parents, which is an added difficulty for the selection.

3.2. General and Specific Combining Abilities

The mean squares and significant effects for general combining abilities (GCAs) and specific combining abilities (SCAs) derived from the analysis, along with their interactions with environments are summarized in Table 7.

Table 7. Mean squares and significant tests of general combining abilities (GCAs) and specific combining abilities (SCAs) for agronomic and quality traits across three environments.

| Variation Sources | DF | PM     | TW     | SG       | CC        |
|-------------------|----|--------|--------|----------|-----------|
| Site              | 2  | 22.43 ** | 3924766 ** | 0.00312 * | 14.85 ** |
| Rep (Site)        | 3  | 1.04 ns  | 30816 ns | 0.00011 * | 0.32 ns   |
| GCA               | 5  | 6.75 **  | 47304 ns | 0.00026 ** | 0.67 ns   |
| SCA               | 9  | 1.99 *   | 51102 ns | 0.00007 ns | 0.67 ns   |
| GCA*Site          | 10 | 0.71 ns  | 67421 ns | 0.00004 ns | 0.74 *    |
| SCA*Site          | 18 | 0.72 ns  | 55100 ns | 0.00005 ns | 0.55 *    |
| Error             | 42 | 0.46    | 46182   | 0.00004   | 0.29      |
| GPR               | 0.87 | 0.65 | 0.88 | 0.67 |

DF, degrees of freedom; PM, plant maturity; TW, tuber weight; SG, specific gravity; CC, chip color; GPR, general predicted ratio GCA/SCA; * and ** significant at p ≤ 0.05 and p ≤ 0.01, respectively; ns not significant.

From the analysis, we see that there was not a significant interaction between the effects of GCA and site for most of the traits, except for CC, for which the analysis detected a slight significant effect. The same results apply to the interaction between the effects of SCA and site.

Regarding the agronomic traits, the partition of the significant genetic variance for PM from the ANOVA in these trials shows that the effects are due to both GCA (F (5,10) = 9.56, p < 0.01) and SCA (F (9,18) = 2.76, p < 0.05), and both mean squares are significant without influence of G×E interactions. Since we did not detect a significant effect for the main factor genotype for TW, the partition of the variance confirms no significant effect for GCA and SCA.

For quality traits, however, the effects are somewhat different. The main-effects analysis showed that the significant genetic variance for SG seems to be only due to GCA effect (F (5,10) = 5.75, p < 0.01), because the SCA effect is not significant. CC is the only trait for which it detected a slight significant effect of the interactions GCA×E (F (10,42) = 2.59, p < 0.05) and SCA*E (F (18,42) = 1.93, p < 0.05), and there is no significant effect for the main factors GCA and SCA.

Estimates of GCA effects and the mean values of each trait for each genotype parent, the general means, and the standard error for means, and for GCA estimates, are shown on Table 8.
Table 8. Mean values and estimates of GCA effects and its standard errors of six parental genotypes across three sites for agronomic and quality traits.

| Genotype | PM Means | GCA | TW Means | GCA | SG Means | GCA | CC Means | GCA |
|----------|----------|-----|----------|-----|----------|-----|----------|-----|
| Caesar   | 4.745    | -0.050 ns | 1523.86 | 68.23 ns | 1.0809 | -0.0050 *** | 5.572 | -0.096 ns |
| Hertha   | 4.719    | -0.083 ns | 1494.60 | 31.65 ns | 1.0931 | 0.0019 ns | 5.723 | 0.092 ns |
| Tomensa  | 4.927    | 0.178 ns  | 1430.98 | 47.87 ns | 1.0933 | 0.0023 ns | 5.614 | -0.044 ns |
| Atlantic | 5.535    | 0.938 *** | 1448.65 | -25.78 ns | 1.0944 | 0.0036 **  | 5.886 | 0.296 ** |
| 95P87-4  | 4.422    | -0.454 *** | 1441.83 | -34.30 ns | 1.0893 | -0.0028 *  | 5.528 | -0.152 ns |
| 95P17-3  | 4.361    | -0.529 *** | 1475.73 | 8.07 ns  | 1.0916 | 0.0001 ns | 5.572 | -0.097 ns |
| General Means | 4.785 |       | 1469.28 |       | 1.0916 |       | 5.649 |       |
| SE       | 1.249    | 0.126 | 370.91  | 40.04 | 0.0113  | 0.0011 | 0.882  | 0.100 |

PM, plant maturity; TW, tuber weight; SG, specific gravity; CC, chip color; *, **, and *** significant at $p \leq 0.05$, $p \leq 0.01$, and $p \leq 0.001$, respectively; ns not significant.

Looking at agronomic traits, for plant maturity (PM) GCA significant effects are found on several parents. Thus, for plant maturity, Atlantic shows a GCA significant positive effect ($t (5) = 7.45$, $p < 0.001$) of 0.938, giving earlier progenies than any other parent, while both advanced clones 95P87-4 and 95P17-3 show significant negative effects ($t (5) = -3.60$, $p < 0.001$ and $t (5) = -4.20$, $p < 0.001$, respectively), with GCA effects of $-0.454$ and $-0.529$, respectively, giving the latest progenies. Neither of the other parents shows a GCA significant effect.

For TW, no GCA significant effect for any parent was detected, and this is in agreement with the results of the ANOVA. Despite this, the varieties Caesar and Hertha exhibited the highest GCA effects for TW, making them suitable candidates for TW improvement in progenies, whereas Tomensa and 95P17-3 showed the lowest GCA effects.

Regarding the quality traits, there are significant differences between GCA effects for different parents. Thus, for SG, the cultivar Atlantic has the significant higher positive GCA effect ($t (5) = 3.13$, $p < 0.01$), whereas the cultivar Caesar and the advanced clone 95P87-4 have significant negative GCA effects ($t (5) = -4.37$, $p < 0.001$ and $t (5) = -2.43$, $p < 0.05$, respectively).

Looking at chip color (CC), even though the analysis showed a statistically significant GCA × site interaction, the positive significant GCA effect ($t (5) = 2.98$, $p < 0.01$) found for the cultivar Atlantic should be taken into account, considering that it is the best positive GCA estimate for CC together with the Hertha cultivar. All the other parents showed negative GCA estimates.

As for the SCA effect, the estimates obtained are presented in Table 9.

The ANOVA revealed that there were significant effects of the main factor SCA for PM, but not for TW, SG, and CC. Moreover, for CC, significant interactions were detected for the GCA × site and SCA × site effects.

Regarding the SCA effect for agronomic traits, as for PM, the crosses Caesar × 95P87-4, Hertha × 95P17-3, Tomensa × 95P17-3, and Atlantic × 95P87-4 were the ones that showed significant differences and produced significantly late progenies. No other crosses showed significant SCA effects, but the highest positive values of the SCA estimates (meaning they produced early progenies) were found in the Caesar × Atlantic and Hertha × Tomensa crosses.

In spite of not being significant differences in the SCA effects for TW, the crosses with higher estimates positive values for this trait were Caesar × Tomensa and Atlantic × 95P17-3, while the lowest SCA estimate values were for the crosses Tomensa × 95P17-3 and Caesar × 95P17-3.

In the same way, although the analysis did not find significant differences between the estimates of SCA for the quality trait SG, two crosses—Caesar × 95P17-3 and Tomensa × 95P87-4—show significant differences between the values of the estimates of SCA, which are precisely the lowest values of the SCA estimates.
Table 9. SCA estimates and its standard errors of agronomic and quality traits.

| ID | Cross Parents | PM  | TW  | SG  | CC  |
|----|---------------|-----|-----|-----|-----|
| 12 | Caesar Hertha | 5.506 | 1509.755 | 1.0904 | 5.506 |
| 13 | Caesar Tomensa | 5.733 | 1633.289 | 1.0887 | 5.733 |
| 14 | Caesar Atlantic | 6.171 | 1464.861 | 1.0908 | 6.171 |
| 15 | Caesar 95P87-4 | 5.515 | 1542.169 | 1.0854 | 5.515 |
| 16 | Caesar 95P17-3 | 4.937 | 1469.222 | 1.0825 | 4.937 |
| 23 | Hertha Tomensa | 5.660 | 1527.361 | 1.0992 | 5.660 |
| 24 | Hertha Atlantic | 6.139 | 1498.985 | 1.0966 | 6.139 |
| 25 | Hertha 95P87-4 | 5.373 | 1405.791 | 1.0889 | 5.373 |
| 26 | Hertha 95P17-3 | 5.936 | 1316.987 | 1.0957 | 5.936 |
| 34 | Tomensa Atlantic | 5.939 | 1332.219 | 1.0971 | 5.939 |
| 35 | Tomensa 95P87-4 | 5.276 | 1345.062 | 1.0899 | 5.276 |
| 36 | Tomensa 95P17-3 | 5.462 | 1316.987 | 1.0957 | 5.462 |
| 45 | Atlantic 95P87-4 | 5.615 | 1546.195 | 1.0953 | 5.615 |
| 46 | Atlantic 95P17-3 | 5.615 | 1546.195 | 1.0953 | 5.615 |

The general mean of all progenies for PM was 4.79, which is equivalent to a medium-late maturity. The progenies of Caesar × Atlantic and Hertha × Atlantic obtained the earliest plant maturity values, (Table 10) medium–early, whereas Caesar × 95P17-3 and Tomensa × 95P87-4 were the later maturity progenies, medium–late maturity cycle. This
is in accordance with the significant genotype effects for this trait and its GCA and SCA variance effects.

The TW varied from 1633.30 to 1317.00 g/plant, with a general mean of 1469.28 g/plant. The crosses with the highest yields were Caesar × Tomensa and Atlantic × 95P17-3, tuber weight, while the lowest yields corresponded to the progenies of the crosses Tomensa × 95P17-3 and Tomensa × Atlantic tuber weight.

For quality traits, the SG ranged between 1.09919 and 1.08253. The highest values for SG were obtained by the crosses Hertha × Tomensa and Tomensa × Atlantic, while the lowest values were for the crosses Caesar × 95P17-3 and Caesar × 95P87-4. For this trait in these trials, the genotype effect is clearly marked, as expected from the analysis of variance, where genotype factor was clearly significant, and from the partition of the variance, GCA was the only significant effect for this trait, with Atlantic being the best significant combiner parent and Caesar and 95P87-4 the worst one.

In terms of the color of chips, the general mean for this trait was 5.65, and the crosses with the highest CC means, both above 6, were Caesar × Atlantic and Hertha × Atlantic. The worst scores were for the cross Caesar × 95P17-3 and for Tomensa × 95P87-4. This agrees with the significant GCA estimate for Atlantic cultivar, which participates in almost the best crosses, and with the significant negative SCA estimate of the cross Caesar × 95P17-3, with the lowest score for CC, even if significant effects of GCA × site and SCA × site were detected in the analysis, interactions that are commented upon in Section 4.1.

3.3. Broad-Sense Heritability

Broad-sense heritability (H²), defined as the ratio of genetic variance to the total phenotypic variance, was calculated from the combined analysis of variance, from the values of the variances of the GCA and SCA and their interactions with the environment for this set of genotypes. The results of H² and their 95% confidence intervals are presented on Table 11.

| PM | TW | SG | CC |
|----|----|----|----|
| H² | 0.90 | 0.52 | 0.82 | 0.40 |
| CI (Upper) | 0.92 | 0.62 | 0.87 | 0.60 |
| CI (Lower) | 0.60 | −0.85 | 0.35 | −0.93 |

PM, plant maturity; TW, tuber weight; SG, specific gravity; CC: chip color.

Regarding the agronomic traits, the H² results showed a high estimate of broad-sense heritability for a PM trait of 0.90 (0.60, 0.92) and a low value of H² for a TW of 0.52 (−0.85, 0.62). Furthermore, the broad-sense heritability estimates for the quality traits analyzed were 0.82 (0.35, 0.87) for SG, and a low value of 0.40 (−0.93, 0.60) for CC.

Values of general predicted ratios (GPRs) were also calculated for the agronomic and quality traits of this trial (Table 7). The ratio GCA/SCA obtained for all the traits was quite high; for PM, it was 0.87, which is similar to that obtained for SG, 0.88. Moreover, for the rest of the analyzed traits, it was quite high, reaching a value of 0.65 and 0.67 for TW and CC, respectively. These results indicate a clear importance of the additive gene effects over non-additive gene action for all the traits analyzed, complementing the information provided by the broad-sense heritability results.

4. Discussion

Breeding for quality in potatoes is a challenging task to achieve, as there is a large number of quantitatively inherited traits involved, and the resulting phenotypes are the outcome of a tetrasomic inheritance and highly heterozygous complex genotypes, with traits expressing interactions among a large number of genes [3,42,43]. The diallel approach has been used in several potato research works to analyze a number of traits of economic importance, including those related to processing quality [44]. The diallel results offer
the necessary information for the breeder to understand the genetic control of the trait of interest, and, at the same time, a base population is generated in order to start a breeding line [14,16,44,45].

The knowledge of the genetic or environmental effects and their interactions that affect commercial and processing quality traits of interest is of great importance for making the best genotype choice for breeding programs.

4.1. Analysis of Variance, GCA, and SCA Effects

The combined ANOVA of the half diallel experiment indicates that the main factor site effect was significant for all traits, pointing out the clear influence of the environment on the results of a polyploid species such as the potato. The analysis of genetic effects found only a slightly significant interaction genotype × site for chip color, but it did not find significant interactions for the rest of the analyzed traits (Table 6).

Mean squares of the main factor genotype were found significant for plant maturity and for specific gravity. GCA was the largest variance component for both traits, although the SCA component contributes also to the variation of PM. For the weight-of-tubers trait, the analysis did not find genotype to have a significant effect, neither G × E significant interaction. Since there is no common pattern for most of the analyzed traits, each trait is discussed here separately.

4.1.1. Plant Maturity

For PM, the analysis detects a significant genotype effect (Table 6), and this effect can be assigned to both variance components, since significant effects were found for GCA and SCA, although GCA was the largest component (Table 7). Previous works do not show a clear trend for this trait. In crosses between S. t. tuberosum parents, significant GCA and SCA variances were observed for plant maturity, with GCA being the most important component [46,47]. A similar result was found for DAF (days-to-flowering trait, a measure of earliness) in a set of progenies that included genotype parents from the International Potato Centre (CIP) likely to have some S. t. andigenum genetic background [48]; and in related research with similar parental genotypes, GCA and SCA components were found significant for earliness in the analyzed progenies [49]. These results differ from those of Reference [30], which found significant effects of GCA (additive genetic variance) for foliage maturity, but they did not find non-additive effects (SCA non-significant) in the genetic analysis of this trait in a set of diploids crosses involving parents’ genotypes with S. t. tuberosum and S. t. andigenum genetic background. Similarly, only additive effects for plant maturity were found in 4x-2x crosses of diploid potato hybrids carrying S. phureja genes [51]. Similar results were found in crosses between male FDR diploid clones and 4x females, both with wide Solanum species genetic background, which are likely to be due to the broad genetic base of the parents used in the study [52]. Additive gene effects then, seem to be more important for plant maturity, since even though SCA component may contribute to the variation, GCA variance was the most important source of variation for this trait. This is reflected also in the GCA/SCA ratio (GPR value [39]) of 0.87 for this trait (Table 7), indicating that the additive gene action makes a greater contribution to the expression of this trait than non-additive gene action. When GCA is large in relation to SCA, it is not only possible to identify the superior crosses but also the better parents. These results agree with the knowledge of genes involved in crop earliness, a trait that, as stated to by Reference [53], is due to a dominant allele with additive effects.

Cultivars and/or advanced clones with significant GCA should be selected as superior parents for crossing for traits with high heritability. According to the obtained results (Table 8), the best combiners for late maturity (meaning high-yielding clones, because the growing cycle is longer) are the two advanced clones 95P87-4 and 95P17-3. In contrast, the cultivar Atlantic is the best parental source for progeny earliness, with a high positive significant GCA effect. This is interesting in terms of developing earlier varieties with good chip processing quality. It may seem contradictory because earliness is associated with a
yield reduction, but in markets where the tuber stock becomes depleted around the end of July and the main harvest season begins in mid-September (as in the north of Spain), an early chiper variety can be a very valuable resource.

The advanced clones 95P17-3 and 95P87-4 breed significantly later progenies, with PM means of 4.36 and 4.42, respectively, for all their progenies (Table 8). Both advanced clones produced progenies with significantly late maturity. GCA estimates for the other genotypes showed that only Tomensa, together with Atlantic, gave rise to short-cycle clones. The other two cultivars, Caesar and Hertha, together with both advanced breeding clones, gave rise to later progenies.

4.1.2. Weight of Tubers

Yield has been defined in many ways depending on the experiment carried out. We refer to this trait here as the total weight of tubers per plant, while in other works the analysis of different components of yield has been carried out individually, such as number of tubers, average tuber weight, or tuber size.

The results of the analysis of our trials for TW showed a significant effect of environment, and this is in agreement with other works in which the environment was described as having an important influence on yield [48,54,55], while no significant effect of the genotype x site interaction was detected (Table 6). G × E interactions have been identified as important sources of variation for tuber yield in potato tetraploid clones [54–59] that are of importance for the selection of adapted genotypes. In this regard, the work of Reference [60] showed GCA preponderance, but also a significant GCA × site interaction for total tuber weight. In the diallel analysis of Reference [61], the additive effects were of greater importance in the seed site trial, while they were of a similar magnitude to the non-additive effects in the ware site trial, hence the importance of a multi-environment analysis.

The main factor genotype was not found to be significant in our group of parents; therefore, no significant effects for GCA or SCA were found. These results are in agreement with those reported by Reference [62], where the combining ability effects for yield traits were generally non-significant in progenies from crosses between materials with S. t. tuberosum genetic background. However, significant GCA and SCA variances for TW have been found in several different environmental situations. Earlier works on inheritance of potato yield showed that the SCA effect was the largest component of the variance [46,63,64], as well as in some modern works [65]. Subsequent research showed divergences between the different authors, especially when different components of yield are considered. Only additive genetic effects were found for total yield in interploidy crosses [66] or in crosses involving “neotuberosum” germplasm [67], or crosses among S. t. andigenum and S. t. tuberosum group parents [50]. However, predominance of GCA effects over SCA were found in the same work for average tuber weight, a yield component [50], or in other research works where it was detected for tuber number [68] and total tuber weight [47,48,68]. Similar significant effects of both GCA and SCA were found in crosses where parents had a broad genetic background [51,52] for total tuber yield.

From our results, the variance component for the main factor genotype is of the same magnitude as that of the experimental error, and the variance component for SCA was not significant, just as it was not for GCA; hence, parents are not consistent in transmitting yielding ability to their offspring. For instance, 95P17-3 was a parent of the second-highest and the lowest-yielding progeny, and 95P87-4 was a parent of the third-highest and the third-lowest yielding progenies (Table 10). It is not possible then to determine if there is a significantly better combiner in our set of plant materials for total tuber yield. The stability of the tuber weight of the genotypes of our crosses can be explained by observing that no significant differences were detected between progenies. There seems to be insufficient diversity in our set of genotypes to develop better, higher-yielding progenies, even when broader genetic bases have been used to deal with perceived plateaus in progress for this trait.
However, and despite this lack of significance, an indication of the relative importance of the variation due to GCA can be hinted from the components of variance shown in Table 7. The moderately high GPR index value of 0.65 indicates that the additive variance is still greater than the variance due to non-additive effects, so it can be said that it would be possible to perform a selection of the best parents, as high ratios of GCA/SCA mean that the additive gene action makes a greater contribution to the expression of this trait than non-additive gene action.

From Table 8, we can see that genotypes that present the highest estimate for GCA were Caesar (68.23) and Hertha (31.65) varieties that stand out from the rest of parents, whereas the lowest estimates were for Tomensa (−47.87) and 95P87-4 (−34.30). Specific crosses that rank well for total yield include the most performant genotypes for GCA, such as Caesar × Tomensa and Hertha × Tomensa, but we could find also specific crosses with good results that were participated by genotypes that had a not especially good GCA effect, such as Atlantic × 95P17-3 or Caesar × 95P87-4; and crosses between good GCA combiners that had bad results, such as Caesar × Hertha (Table 9).

Yield is a trait likely to be highly polygenic [16] and difficult to select for. Varieties developed over the last years have reached a plateau, with similar performance for many years, indicating minimal genetic gains in yield after several decades of breeding and selection [14]. The absence of marked genetic gain has been largely attributed to the complex genetics associated with autotetraploid potato, such as high heterozygosity, genetic background, and severe inbreeding depression among other. Diploid breeding schemes have been adopted to overcome these obstacles [69]. An effort can also be made at the tetraploid level, improving conventional potato breeding with better techniques for quantitative trait selection [14,44].

4.1.3. Specific Gravity

This is one of the most important traits that define a genotype’s aptitude for processing. The ANOVA of our trials detects—as for all of the other traits—a significant effect of environment, which accounts for a large proportion of the total variation. A significant effect of the main factor genotype was also found, whereas the genotype x site interaction was not found to be significant (Table 6). The significant genotype effect can be assigned exclusively to the parent genetic effect, as the GCA variance component was found to be significant, with no influence of SCA or interactions (Table 7). These results confirm most of the previous works on this trait that reported GCA as the only significant effect for specific gravity [47,50,62], with the SCA effect either being non-significant or very small in scope [60,63]. SCA significant effect for SG was only reported in families derived from interploidy 4x–2x crosses [51]. These works showed that the G × E interaction for specific gravity is generally low, so rankings of cultivars do not change across years and production environments [70–72]. As it can be expected from these results, the GPR index was very high, reaching a value of 0.88 (Table 7), which indicates the importance of additive effects, allowing an efficient parental selection for SG.

As the GCA effect was the main significant factor, from the genotypes of our trials, the best result is for the Atlantic cultivar, for which the analysis found a positive significant GCA effect of 0.00360, with a SG mean for all its progenies of 1.0944 (Table 8) equivalent to 23.25% of dry matter in the tubers. This cultivar as parent significantly increased the specific gravity of its progenies, while for 95P17-3, its GCA was positive but not significant; and for 95P87-4, it was significant and negative, meaning that progenies from both parents will not have positive effects on the SG results, as can be seen in Table 10, where the crosses with these genotypes are mostly ranked in the last positions. Only when crossed with good combiners such as Atlantic, progenies showed better SG values. It is worth noting that Atlantic showed the highest significant effects for earliness, and early maturing cultivars typically do not produce as much dry matter as late maturing clones, which have more time to accumulate photosynthates [71]. Usually, late maturing cultivars are preferred for
processing quality, but this genotype shows good performance of progenies for both traits and must be considered for the breeding program.

4.1.4. Chip Color

This is another important trait for potato processing quality. Chip color depends mainly on the content of reducing sugars (fructose and glucose especially) in the tuber tissue, and cold storage (below 8 °C) may induce their accumulation [73]. Two genetic components explain the expression of chip color: overall capacity and stability at low temperatures [74,75]. Since selection for overall chip quality has been demonstrated to be more important than selection for stability [76], the focus of this work has been in the assessment of chip color just after harvest.

The ANOVA showed a significant effect of the environment which was the largest effect, as for all the other traits. Genotype x environment interaction effect was detected as significant, but the analysis did not find significant effect for the main factor genotype (Table 6). The interactions GCA x site and SCA x site were found significant (Table 7). It is known that the environment has a large impact on chip color [71]. A previous work reported that G x E interaction for chip color was found significant, but the environmental effects due to the growing sites did not appear to be a major source of interaction, while the storage regimes showed much greater differences between them than the experimental sites [77].

This result differs from that reported by Reference [78], which found a large significant interaction for chip color between genotype and environment, and a significant interaction genotype x storage duration, after progeny testing of tetraploid S. t. tuberosum families.

From previous works on the genetic components of the variation for CC, GCA was found to be the largest component, and SCA was also found to be significant but to a much lesser extent [47]. GCA x environment and SCA x environment interactions were also significant for CC in other works [62], meaning that additive and non-additive genes effects were not as efficient as they should be, since the influence of the environment modifies the expression of the phenotype. Under these conditions, the selected genotypes should be evaluated in multiple environments and storage conditions to ensure a good response.

This can be seen in our results, which show different parental genotypes expression in the growing sites, which is the source of the G x E interactions. This can be illustrated by looking at crosses Caesar × 95P87-4, Tomensa × Atlantic, Tomensa × 95P17-3 and Atlantic × 95P17-3 that showed a higher value of chip color in PA04 site than in BU04 site, when, for most of the crosses, the BU04 site gave better fry-quality results than the PA04 site. Moreover, the cross Tomensa × 95P87-4 showed higher chip-color means in BU04 site than in BU03 site, but also in PA04 site than in BU03 site. Thus, parental genotypes were not consistent over environments, and 5 out of 15 crosses resulted in non-expected chip-color means.

The presence of these interactions agrees with previous results [62,77] that were able to demonstrate a significant effect of genotype x site interaction independently of the storage temperature on potato chip color, but the lack of significant genotype effects from our experiments is likely to indicate a narrow genetic base in our genotypes set.

4.2. Broad-Sense Heritability

Heritability estimates are obtained from the genetic and environmental variances and are, therefore, only suitable for the genotypes involved in the trial. Heritability is never a fixed value for a given trait; it is the ratio between the variation caused by genetic factors and that caused by genes, environmental effects, and the interactions between genotypes and environments. In vegetatively propagated species such as potatoes, heritability in the broad sense, that which includes all additive and non-additive genetic effects, is of great importance, since it is possible to take advantage of all this genetic variation, which is fixed in the F1 [14,24].
From previous works, very different estimates of broad-sense heritability have been obtained for a given trait, depending on the genetic content of the genotypes under trial, as well as the environments considered, since the more the experimental noise is minimized, the better the heritability estimates will be. $H^2$ for plant maturity trait from our progenies showed a high estimate of broad-sense heritability of 0.90 (95% confidence interval 0.60, 0.92). Not many works on earliness inheritance have been reported, [16,47,49,58,79], but this result is in line with most of the published results, which report $H^2$ values from 0.54 to 0.97. In general, these relatively high values indicate that, for earliness, there is a sufficiently large genetic component in this group of parents as to be used for breeding.

For yield, however, the situation is quite different. Results of $H^2$ from previous works reflect a wide variation, from 0.34 to 0.96, but most of them indicate low values, as expected for a trait strongly influenced by the environment [42,44,45,47,49,80]. A low value of broad-sense heritability for tuber weight of 0.52 was also obtained from the analysis of our progenies (95% confidence interval −0.85, 0.62), and it might be explained by a low genetic variance for tuber weight in our set of genotypes, as well as by a high environmental variation, that accounts for most of the total variation in the trials, impeding the detection of any genetic effect. This is in line with other experimental results indicating that genetic gain in traits with moderate-to-low heritability, such as yield, is quite low and progeny testing results in small improvement [14].

Being a trait of great importance to the processing industry, tuber specific gravity has been widely studied, and it is considered a trait of a medium–high heritability. The results of $H^2$ from previous studies [42,47,58,72,81–84] are in a range of 0.24 to 0.91, although most are between the values of 0.65 to 0.85. We estimated a $H^2$ value of 0.82 (95% CI: 0.35, 0.87), which agrees with the idea of the importance of the genetic component for this trait, which indicates that we can make an adequate selection of clones with high specific gravity allowing for genetic gains to improve this trait in our population.

Chip color is also an important trait, and we focused our study on the chip color directly after harvest; it has also been a trait largely studied. Broad-sense heritability estimates from previous works [44,47,81,83–85] are in a range of 0.59 to 0.94, so this trait is generally considered to be of high heritability. However, the results of our tests showed a low $H^2$ value for this trait of 0.40 (95% CI: −0.93, 0.60), differing widely from what we expected. This could also be explained—as in the case of the tubers yield trait—by a low genetic variance in our set of genotypes, and by a high environmental variance, as can be deduced from the ANOVA mean squares that showed a significant interaction between genotypes and environments.

Low heritability values in most experiments were generally due to the presence of environmental interactions, suggesting that an assessment of parents’ value should be performed in as many environments as possible in order to identify parental genotypes with the broadest adaptation, and hence higher genetic effects.

The phenotypic selection used in progeny testing can provide effective identification of the main genetic factors of quantitative potato traits [16]. For several years, the genomic estimated breeding values (genomic selection) have been developed for complex potato traits [86], as for starch quality and chipping quality [87]. The genomic selection is a useful tool, as an indirect selection method, to accelerate genetic gain in breeding programs [88].

5. Conclusions

Through this work, the evaluation of a new germplasm that could be part of a group of parents that provided improved characteristics to a potato breeding program was carried out. These traits cannot be deduced from the behavior of the parents themselves, but rather require an analysis of the progenies produced, the diallelic mating design having made possible the discovery of their ability to transmit agronomic and quality traits to their offspring.

Significant effects of GCA and SCA were found for a trait such as earliness, only GCA effects were found for specific gravity, and interactions of both GCA and SCA effects with
the environment were found for the chip color trait. However, no genetic effects were detected for yield. Where GCA significant effects were found, additive genetic effects are predominant; thus, for those traits, it is possible to use these genotypes as parents to obtain better progenies.

For plant maturity, the genotype Atlantic had a positive GCA effect and was the best parent to get earlier progenies, while advanced clones 95P87-4 and 95P17-3 had negative GCA effects and were the best parents to develop later progenies. A quite high broad-sense heritability value was obtained for this trait, so it could be possible to get genetic gains in plant maturity with these parents.

A link between earliness and specific gravity was found through the Atlantic genotype, for which the results confirm that this genotype obtained the highest positive value of the GCA effect and performs as a good parent also for the specific gravity. Together with the Tomensa genotype, both gave rise to most of the best progenies with higher specific gravity values. However, advanced breeding clone 95P87-4 together with variety Caesar received the highest negative GCA value for specific gravity, while 95P17-3 was almost neutral for this trait.

None of these genotypes were found to be relevant to improve the yield of the progenies; our trials did not detect significant effects for GCA or SCA. Environmental variation is likely to have been very high, and, together with some lack of genetic diversity in our set of genotypes, it may have produced this result. This, together with the very low value of the broad-sense heritability obtained for this character, does not allow us to ensure an improvement in the productivity of the crosses of these parents.

The environmental interactions (significant GCA × site and SCA × site) found for the chip color trait limit breeding progress. The genotypes did not show their potential, as interactions modify the phenotype expression, even though the genotype Atlantic, for instance, was found to be a good parent with a high GCA value and some crosses that involved this genotype obtained good overall means for chip color. However, there is no confidence in this genotype to be a better parent than any other, because of the interactions.

Putting all of these results together, we see that the Atlantic is the only genotype that could be considered for selection as a superior parental genotype for earliness and chip quality, while the advanced breeding clones 95P87-4 and 95P17-3, which have a genetic background from \textit{S. t. andigenum}, in spite of being good parents for late maturity, cannot be assured to be especially good parents for chip quality attending the environmental effects. None of them is a clear candidate for good yielding parents, either.

Our results confirm that severe selection for tuber quality traits and yield in early generations could not be recommended because of the strong influence of environment on these traits. Sufficient trials in selected environments should be carried out to have an assessment of genotype × environment interactions, especially for quality traits.

Progeny testing resulted in being a very good tool to get information on the performance of the parental genotypes, and it confirms that the early assessment of parents in multiple locations should be performed to identify genotypes that are able to transfer their positive traits to their progenies, while also evaluating their adaptation.

**Author Contributions:** Conceptualization, R.R.d.A., J.M.C. and M.R.-Q.; methodology, J.M.C., A.C., F.O. and R.R.d.A.; data collect, R.R.d.A., A.C. and F.O.; data curation, R.R.d.A.; writing—original draft preparation, R.R.d.A.; writing—review and editing, J.M.C.; supervision, J.M.C. All authors have read and agreed to the published version of the manuscript.

**Funding:** This research was funded by the regional government “Junta de Castilla y León” and the regional potato seed production cooperatives of Castile and Leon.

**Data Availability Statement:** The data presented in this study are available upon request from the corresponding author.

**Acknowledgments:** We wish to thank the Appacale’s work crew for their support in trials: Elena Franco, Carmen Abajo, Jose Ramón Bravo, Silvia Miguelez, Milagros Melgar, and Luis Javier Calderón.
We also thank to Simón Isla, for his general support. Javier Legorburu is acknowledged for critically reading the manuscript.

Conflicts of Interest: The authors declare no conflict of interest.

References

1. Bradshaw, J.E. Potato-Breeding Strategy. In Potato Biology and Biotechnology; Vreugdenhil, D., Bradshaw, J., Gebhardt, C., Govers, F., Mackerron, D.K.L., Taylor, M.A., Ross, H., Eds.; Elsevier Science B.V.: Amsterdam, The Netherlands, 2007; pp. 157–177, ISBN 978-0-444-51018-1.

2. Jansky, S.H.; Spooner, D.M. The Evolution of Potato Breeding. In Plant Breeding Reviews; Goldman, L., Ed.; John Wiley & Sons, Inc.: Hoboken, NJ, USA, 2018; Volume 41, pp. 169–214. ISBN 9781119414735.

3. Bonierbale, M.W.; Amoros, W.R.; Salas, E.; de Jong, W. Potato Breeding. In The Potato Crop: Its Agricultural, Nutritional and Social Contribution to Humankind; Campos, H., Ortiz, O., Eds.; Springer International Publishing: Cham, Switzerland, 2020; pp. 163–217. ISBN 978-3-030-28683-5.

4. Bradshaw, J.E.; Mackay, G.R. Breeding Strategies for Clonally Propagated Crops. In Potato Genetics; Bradshaw, J.E., Mackay, G.R., Eds.; CAB International: Wallingford, UK, 1994; pp. 467–497. ISBN 0-85198-869-5.

5. Bradshaw, J.E. Review and Analysis of Limitations in Ways to Improve Conventional Potato Breeding. In Potato Biology and Biotechnology; Bradshaw, J., Gebhardt, C., Govers, F., Mackerron, D.K.L., Taylor, M.A., Ross, H., Eds.; Elsevier Science B.V.: Amsterdam, The Netherlands, 2007; pp. 157–177, ISBN 978-0-444-51018-1.

6. Schönhals, E.M.; Ortega, F.; Barandalla, L.; Aragones, A.; Ruiz de Galarreta, J.I.; Liao, J.-C.; Sanetomo, R.; Walkemeier, B.; Tacke, E.; Ritter, E.; et al. Identification and Reproducibility of Diagnostic DNA Markers for Tuber Starch and Yield Optimization in a Novel Association Mapping Population of Potato (Solanum Tuberosum L.). Theor. Appl. Genet. 2016, 129, 767–785. [CrossRef] [PubMed]

7. Khan, M.S.; van Eck, H.J.; Struik, P.C. Model-Based Evaluation of Maturity Type of Potato Using a Diverse Set of Standard Cultivars and a Segregating Diploid Population. Potato Res. 2013, 56, 127–146. [CrossRef]

8. Ruiz de Arcaute, R.; Carrasco, A.; Ortega, F.; Isla, S. Potato Breeding Programme in APPACALE S. A. (Castilla y León, Spain). Plant Breed. Seed Sci. 2000, 44, 59–66.

9. Ortega, F.; Carrasco, A.; Ortega, F.; Isla, S. Potato Breeding Programme in APPACALE S. A. (Castilla y León, Spain). Plant Breed. Seed Sci. 2000, 44, 59–66.

10. FAO—Food and Agriculture Organisation of the United Nations FAOSTAT. Available online: https://www.fao.org/faostat/en/#data/QCL (accessed on 22 March 2022).

11. Devaux, A.; Goffart, J.-P.; Petsakos, A.; Kromann, P.; Gatto, M.; Okello, J.; Suarez, V.; Hareau, G. Global Food Security, Contributions from Sustainable Potato Agri-Food Systems. In Proceedings of the Acta Horticulturae, Viterbo, Italy, 30 June 2005; Casa, R., Viola, R., Eds.; International Society for Horticultural Science (ISHS): Leuven, Belgium, 2005; pp. 55–64.

12. Eurostat. The EU Potato Sector—Statistics on Production, Prices and Trade. Available online: https://ec.europa.eu/eurostat/statistics-explained/index.php?title=The_EU_potato_sector_-_statistics_on_production,_prices_and_trade#Processing (accessed on 22 March 2022).

13. Ruiz de Arcaute, R.; Carrasco, A.; Ortega, F.; Isla, S. Potato Breeding Programme in APPACALE S. A. (Castilla y León, Spain). Plant Breed. Seed Sci. 2000, 44, 59–66.

14. Bradshaw, J.E. Review and Analysis of Limitations in Ways to Improve Conventional Potato Breeding. Potato Res. 2017, 60, 171–193. [CrossRef]

15. Kirkman, M.A. Chapter 2—Global Markets for Processed Potato Products. In Potato Biology and Biotechnology; Vreugdenhil, D., Bradshaw, J., Gebhardt, C., Govers, F., Mackerron, D.K.L., Taylor, M.A., Ross, H.A., Eds.; Elsevier Science B.V.: Amsterdam, The Netherlands, 2007; pp. 27–44. ISBN 978-0-444-51018-1.

16. Slater, A.T.; Cogan, N.O.I.; Hayes, B.J.; Schultz, L.; Dale, M.F.B.; Bryan, G.J.; Forster, J.W. Improving Breeding Efficiency in Potato Using Molecular and Quantitative Genetics. Theor. Appl. Genet. 2014, 127, 2279–2292. [CrossRef]

17. Ferrández-Northcote, E.N. Mejoramiento Por Resistencia a Los Principales Virus de La Papa. Rev. Lat. Papa 1991, 4, 1–21.

18. Lopez-Vizcon, C.; Ortega, F. Molecular Marker Assisted Selection (MAS) Application in a Small Breeding Company. In Proceedings of the 18th Triennial Conference of the European Association for Potato Research; Santal, J., Valkonen, J.P., Eds.; EAPR: Oulu, Finland, 2011; p. 44.

19. Ortega, F.; Lopez-Vizcon, C. Application of Molecular Marker-Assisted Selection (MAS) for Disease Resistance in a Practical Potato Breeding Programme. Potato Res. 2012, 55, 1–13. [CrossRef]

20. Ortega, F.; Carrasco, A. Germplasm Enhancement with Wild Tuber-Bearing Species: Introgression of PVY Resistance and High Dry Matter Content from Solanum berthaultii, S. gourlayi, S. tarijense and S. vernei. Potato Res. 2005, 48, 97–104. [CrossRef]

21. Ortega, F.; Carrasco, A.; Ruiz de Arcaute, R. Comparison of Solanum Phureja Clones in the Obtention of Primary Dihaploids from Potato. In Proceedings of the Congreso Iberoamericano de Investigación y Desarrollo de Patata—Vitoria-Gasteiz, 3–6 Julio 2000; DFA, DAMA, Eds.; DFA—Diputación Foral de Álava: Vitoria-Gasteiz, Spanish, 2000.

22. Tarn, T.R.; Tai, G.C.C.; De Jong, H.; Murphy, A.M.; Seabrook, J.E.A. Breeding Potatoes for Long-Day, Temperate Climates. Plant Breed. Rev. 1992, 9, 217–332.
54. De Jong, H.; Tai, G.C.C.; Russell, W.A.; Johnston, G.R.; Proudfoot, K.G. Yield Potential and Genotype-Environment Interactions of Tetraploid-Diploid (4x–2x) Potato Hybrids. Am. Potato J. 1981, 58, 191–199. [CrossRef]
55. Affleck, I.; Sullivan, J.A.; Tarn, R.; Falk, D.E. Genotype by Environment Interaction Effect on Yield and Quality of Potatoes. Can. J. Plant Sci. 2008, 88, 1099–1107. [CrossRef]
56. Tai, G.C.C.; Young, D.A. Genotypic Stability Analysis of Eight Potato Varieties Tested in a Series of Ten Trials. Am. Potato J. 1972, 49, 138–150. [CrossRef]
57. Tai, G.C.C. Analysis of Genotype-Environment Interactions of Potato Yield 1. Crop Sci. 1979, 19, 434–438. [CrossRef]
58. Yildirim, M.B.; Çalişkan, C.F. Genotype X Environment Interactions in Potato (Solanum tuberosum L.). Am. Potato J. 1985, 62, 371–375. [CrossRef]
59. Hassanpanah, D. Analysis of GxE Interaction by Using the Additive Main Effects and Multiplicative Interaction in Potato Cultivars. Int. J. Plant Breed. Genet. 2010, 4, 23–29. [CrossRef]
60. Landeo, J.A.; Hanneman, R.E. Heterosis and Combining Ability of Solanum Tuberosum Group Andigena Haploids. Potato Res. 1982, 25, 227–237. [CrossRef]
61. Neele, A.E.F.; Nab, H.; Louwes, K.M. Identification of Superior Parents in a Potato Breeding Programme. Theor. Appl. Genet. 1991, 82, 264–272. [CrossRef]
62. Lynch, D.R.; Tai, G.C.C.; Coffin, R.H. Genetic Components of Potato Chip Quality Evaluated in Three Environments and under Various Storage Regimes. Can. J. Plant Sci. 1992, 72, 535–543. [CrossRef]
63. Tai, G.C.C. Estimation of General and Specific Combining Abilities in Potato. Can. J. Genet. Cytol. 1976, 18, 463–470. [CrossRef]
64. Plaisted, R.L.; Sanford, L.; Federer, W.T.; Kehr, A.E.; Peterson, L.C. Specific and General Combining Ability for Yield in Potatoes. Am. Potato J. 1962, 39, 185–197. [CrossRef]
65. Ruiz de Galarreta, J.I.; Ezpeleta, B.; Pascualena, J.; Ritter, E. Combining Ability and Correlations for Yield Components in Early Generations of Potato Breeding. Plant Breed. 2006, 125, 183–186. [CrossRef]
66. Masson, M.F. Mapping, Combining Abilities, Heritabilities and Heterosis with 4x × 2x Crosses in Potato. Ph.D. Thesis, University of Wisconsin-Madison, Madison, WI, USA, 1985.
67. Rowell, A.B.; Ewing, E.E.; Plaisted, R.L. General Combining Ability of Neo-Tuberous for Potato Production from True Seed. Am. Potato J. 1986, 63, 141–153. [CrossRef]
68. Brown, J.; Caligari, P.D.S. Cross Prediction in a Potato Breeding Programme by Evaluation of Parental Material. Theor. Appl. Genet. 1989, 77, 246–252. [CrossRef] [PubMed]
69. Marand, A.P.; Jansky, S.H.; Gage, J.L.; Hamernik, A.J.; de Leon, N.; Jiang, J. Residual Heterozygosity and Epistatic Interactions Underlie the Complex Genetic Architecture of Yield in Diploid Potato. Genetics 2019, 212, 317–332. [CrossRef] [PubMed]
70. Killick, R.J.; Simmonds, N.W. Specific Gravity of Potato Tubers as a Character Showing Small Genotype-Environment Interactions. Heredity 1974, 32, 109–112. [CrossRef]
71. Jansky, S. Chapter 2—Breeding, Genetics, and Cultivar Development. In Advances in Potato Chemistry and Technology; Singh, J., Kaur, L.B.T., Eds.; Academic Press: San Diego, CA, USA, 2009; pp. 27–62, ISBN 978-0-12-374349-7.
72. Haynes, K.G.; Wilson, D.R.; Kang, M.S. Genotype × Environment Interactions for Specific Gravity in Diploid Potatoes. Crop Sci. 1995, 35, 977–981. [CrossRef]
73. Burgos, G.; zum Feledie, T.; Andre, C.; Kubow, S. The Potato and Its Contribution to the Human Diet and Health. In The Potato Crop: Its Agricultural, Nutritional and Social Contribution to Humankind; Campos, H., Ortiz, O., Eds.; Springer International Publishing: Cham, Switzerland, 2020; pp. 37–74, ISBN 978-3-030-28683-5.
74. Kawchuk, L.M.; Lynch, D.R.; Yada, R.Y.; Bizimungu, B.; Lynn, J. Marker Assisted Selection of Potato Clones That Process with Light Chip Color. Am. J. Potato Res. 2008, 85, 227. [CrossRef]
75. Lynch, D.R.; Kawchuk, L.M.; Yada, R.; Armstrong, J.D. Inheritance of the Response of Fry Color to Low Temperature Storage. Am. J. Potato Res. 2003, 80, 341. [CrossRef]
76. Rak, K.; Navarro, F.M.; Palta, J.P. Genotype × Storage Environment Interaction and Stability of Potato Chip Color: Implications in Breeding for Cold Storage Chip Quality. Crop Sci. 2013, 53, 1944–1952. [CrossRef]
77. Tai, G.C.C.; Coleman, W.K. Genotype × Environment Interaction of Potato Chip Colour. Can. J. Plant Sci. 1999, 79, 433–438. [CrossRef]
78. Hayes, R.J.; Thill, C.A. Genetic Gain from Early Generation Selection for Cold Chipping Genotypes in Potato. Plant Breed. 2003, 122, 158–163. [CrossRef]
79. Bradshaw, J.E.; Hackett, C.A.; Pande, B.; Waugh, R.; Bryan, G.J. QTL Mapping of Yield, Agronomic and Quality Traits in Tetraploid Potato (Solanum tuberosum Subsp. tuberosum). Theor. Appl. Genet. 2008, 116, 193–211. [CrossRef] [PubMed]
80. Rak, K.; Palta, J.P. Influence of Mating Structure on Agronomic Performance, Chip Fry Color, and Genetic Distance Among Biparental Tetraploid Families. Am. J. Potato Res. 2015, 92, 518–535. [CrossRef]
81. Cunningham, C.E.; Stevenson, F.J. Inheritance of Factors Affecting Potato Chip Color and Their Association with Specific Gravity. Am. Potato J. 1963, 40, 253–265. [CrossRef]
82. Freyre, R.; Douches, D.S. Isoenzymatic Identification of Quantitative Traits in Crosses between Heterozygous Parents: Mapping Tuber Traits in Diploid Potato (Solanum spp.). Theor. Appl. Genet. 1994, 87, 764–772. [CrossRef]
83. Haynes, K.G. Heritability of Chip Color and Specific Gravity in a Long-Day Adapted Solanum phureja–S. stenotomum Population. Am. J. Potato Res. 2008, 85, 361. [CrossRef]
84. Neele, A.E.F.; Louwes, K.M. Early Selection for Chip Quality and Dry Matter Content in Potato Seedling Populations in Greenhouse or Screenhouse. *Potato Res.* **1989**, *32*, 293–300. [CrossRef]

85. Werij, J.S.; Furrer, H.; van Eck, H.J.; Visser, R.G.F.; Bachem, C.W.B. A Limited Set of Starch Related Genes Explain Several Interrelated Traits in Potato. *Euphytica* **2012**, *186*, 501–516. [CrossRef]

86. Ortiz, R. Genomic-Led Potato Breeding for Increasing Genetic Gains: Achievements and Outlook. *Crop Breed. Genet. Genom.* **2020**, *2*, e200010. [CrossRef]

87. Sverrisdóttir, E.; Byrne, S.; Sundmark, E.H.R.; Johnsen, H.Ø.; Kirk, H.G.; Asp, T.; Janss, L.; Nielsen, K.L. Genomic Prediction of Starch Content and Chipping Quality in Tetraploid Potato Using Genotyping-by-Sequencing. *Theor. Appl. Genet.* **2017**, *130*, 2091–2108. [CrossRef]

88. Stich, B.; van Inghelandt, D. Prospects and Potential Uses of Genomic Prediction of Key Performance Traits in Tetraploid Potato. *Front. Plant Sci.* **2018**, *9*, 159. [CrossRef] [PubMed]