AGHmatrix: R Package to Construct Relationship Matrices for Autotetraploid and Diploid Species: A Blueberry Example

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Abstract
Progress in the rate of improvement in autopolyploid species has been limited compared with diploids, mainly because software and methods to apply advanced prediction and selection methodologies in autopolyploids are lacking. The objectives of this research were to (i) develop an R package for autopolyploids to construct the relationship matrix derived from pedigree information that accounts for autopolyploidy and double reduction and (ii) use the package to estimate the level and effect of double reduction in an autotetraploid blueberry breeding population with extensive pedigree information. The package is unique, as it can create A-matrices for different levels of ploidy and double reduction, which can then be used by breeders to fit mixed models in the context of predicting breeding values (BVs). Using the data from this blueberry population, we found for all the traits that tetrasomic inheritance creates a better fit than disomic inheritance. In one of the five traits studied, the level of double reduction was different from zero, decreasing the estimated heritability, but it did not affect the prediction of BVs. We also discovered that different depths of pedigree would have significant implications on the estimation of double reduction using this approach. This freely available R package is available for autopolyploid breeders to estimate the level of double reduction present in their populations and the impact in the estimation of genetic parameters as well as to use advanced methods of prediction and selection.

Core Ideas
• We developed an R package for autopolyploids to construct the relationship matrix.
• We estimated the level and effect of double reduction in blueberry.
• The package is unique as it can create A-matrices for different levels of ploidy.
• The package can create A-matrices for different levels of double reduction

Several important agronomic and horticultural crops such as alfalfa (Medicago sativa L.), potato (Solanum tuberosum L.), and highbush blueberry (Vaccinium corymbosum L.) are autotetraploids, with four homologous chromosomes present in each linkage group. As more than two homologous chromosomes exist in autotetraploids, during meiosis chromosome pairing can occur between a pair of randomly chosen chromosomes (bivalents) or between more than two homologous chromosomes (multivalents) (Fisher, 1947). This polysomic...
inference results in different segregation ratios for a
given locus compared with diploid species, as up to four
copies of an allele lead to the possibility of higher orders
of allele interaction (see details in Gallais, 2003). Thus,
considering a biallelic marker, there are five possible states
for a given A allele (referred hereafter as dosage): nulli-
plex, simplex, duplex, triplex, and quadruplex represent-
inging aaaa, Aaaa, AAAa, and AAAA, respectively.
Moreover, the phenomenon known as double reduction,
where sister chromatids segregate into the same gamete,
creates difficulties when studying quantitative or popula-
tion genetics in autotetraploid species. Despite the fact
that double reduction is not well studied, its occurrence
has practical implications in plant breeding because it can
result in increased inbreeding even when two unrelated
individuals are crossed (Mather, 1935; Mather, 1936; Gal-
lais, 2003; Kerr et al., 2012). These challenges, and the fact
that these differences are often ignored in breeding strate-
gies, have been identified as the main reasons why the rate
of genetic improvement has been limited and sometimes
null in autotetraploid species as compared with their dip-
loid counterparts (Brummer, 1999; Katepa-Mupondwa et
al., 2002; Jansky, 2009). As an example, the genetic gain
for yield in alfalfa since 1940 has been between 0 and
0.30% yr⁻¹ on average, while 2% has been estimated in
annual diploid crops (Brummer, 1999).

Breeding autotetraploid species also typically take
longer than diploid species, and the development of
an improved cultivar can take between 10 and 20 yr
(Lyrene, 2008; Bradshaw and Bonierbale, 2010). One
reason is that it takes longer for autotetraploids to elimi-
nate deleterious alleles because of the greater number
of possible states (i.e., aaaa, Aaaa, and AAAA) (Gallais,
2003). Even though progress has been made in these spe-
cies, materialized in the many cultivars released, current
improvement strategies (e.g., phenotypic recurrent selec-
tion) and analysis methods are rudimentary and known
to be inefficient (Slater et al., 2013).

One of such autotetraploid species is blueberry,
including highbush, southern highbush (V. corymbosum
interspecific hybrids), and lowbush (V. angustifolium L.).
Blueberries are an economically important small fruit
crop for the United States. In 2014, 0.25 Tg (543.5 million
pounds) of blueberries were harvested for fresh produc-
tion and valued at $824.9 million (USDA, 2015). United
States production has increased an average of 20% every 2
yr since 2008, while acreage has increased by nearly 75%
between 2005 and 2012. This increase is based in part on
the reputation of blueberry fruit and products as health
foods because of the high amounts of antioxidants such
as anthocyanins. Antioxidants have been correlated with
beneficial health effects in numerous biological systems
including immunology, ophthalmology, cardiology, neu-
rology, metabolism, and inflammation (Cassidy et al.,
2013; Fan et al., 2012; Heim et al., 2012; Krikorian et al.,
2010; Li et al., 2013; Liu et al., 2012; McAnulty et al., 2011;
Shukitt-Hale, 2012; Tipton et al., 2013; Yousef et al., 2013).

The blueberry breeding program at the University of
Florida develops southern highbush blueberry cultivars
(2x = 4n = 48). These hybrid cultivars are derived mainly
from crosses between northern highbush tetraploid cul-
tivars (V. corymbosum) and diploid species (V. darrowii),
with lesser contributions from various other Vaccinium
species such as V. arboreum, V. elliottii, and V. virgatum
(Brevis et al., 2008; Lyrene 1997, 2008; Olmstead et al.,
2013). Many traits under selection in this species are
polygenic (Lyrene 1993) and the few inheritance studies
of tetraploid V. corymbosum and V. corymbosum × V.
darrowii crosses have shown inheritance patterns that
follow expected autotetraploid segregation ratios (Draper
and Scott, 1971; Krebs and Hancock, 1989; Qu and Han-
cock, 1995). Additionally, the degree of double reduc-
tion present in blueberry is not yet known, and previous
reports were not conclusive (Krebs and Hancock, 1989).
The use of quantitative genetic methods for breeding
of blueberries or any other autotetraploid plant is not
as developed as diploid species. In conventional diploid
breeding, the use of linear mixed models, popularly
known as best linear unbiased prediction (BLUP), is a
method used to estimate variance components through
restricted maximum likelihood (REML) and predict
BVs. This methodology was developed by Henderson
in the 1950s (Van Vleck, 1998) and was first applied to
livestock breeding (VanRaden, 2008). In the past two
decades, BLUP has gained popularity in plant breeding,
first with perennial and forestry crops and more recently
with annual crops (Piepho et al., 2008). In this period,
the applicability of BLUP has been tested and adopted
in breeding diploid crops (Bernardo, 1994, 1996; Cossa
et al., 2010; Resende et al., 2012; Massman et al., 2013).
However, its use in many polyploid species, such as
blueberries, has not been explored yet.

One of the main characteristics in the use of REML
and BLUP in breeding is the use of a numerator matrix
(A) containing an estimate of the pairwise relationship
among individuals. This information is used to model
the variance covariance between the populations. Kerr
et al. (2012) developed an extension of the numerator
relationship matrix based on pedigree values (A-matrix)
for autopolyploids. This calculation includes the ploidy
level and w coefficient (proportion of the alleles which
are identical by descent, double reduction). Using this
new tetraploid A-matrix, Slater et al. (2013) found that
higher genetic gains could be obtained for quantitative
traits in autotetraploid potato when compared with the
traditional phenotypic selection. However, there is cur-
rently no software available to construct such matrices so
that autotetraploid breeders can test and implement these
new and more efficient selection methods.

The objective of this study was two-fold: (i) to develop
an R package for construction of an autotetraploid rela-
tionship matrix that considers autopolyplody and double
reduction derived from pedigree information and (ii)
to estimate the level of double reduction present in the
University of Florida blueberry breeding germplasm and
to study its effects on model fitting and genetic parameter estimations. This information will allow the future implementation of BLUP and REML methods to estimate BVs in the breeding program, study of genetic diversity, inbreeding, definition of heterotic groups, etc.

Materials and Methods

Blueberry Breeding Population and Pedigree
The southern highbush blueberry population used in this study was generated from the breeding program at the University of Florida. This population was developed through 124 controlled crosses of 148 selected parents made in February 2011. Seeds were extracted from the resulting mature fruit, cold stratified for 5 mo, and planted in November 2011 as a family in 2-L pots in a greenhouse. One hundred seedlings from each family were transplanted to trays in January 2012 and planted in May 2012 in a high-density (~20,000 plants per 0.2 ha) nursery at the Plant Science Research and Education Unit in Citra, Florida. In May 2013, five to 32 plants were selected from each family, and the remaining plants were removed from the planting, leaving 1996 plants.

The pedigree of the University of Florida blueberry breeding program was assembled using internal pedigree records, the NCGR–Corvallis Vaccinium Catalog (National Center for Genome Resources–Corvallis, 2012), and the Brooks and Olmo Register of Fruit and Nut Varieties (Brooks and Olmo, 1952, 1997). The file was ordered chronologically beginning with the founding parents in 1908. The pedigree file contains 7755 lines with annotated pedigree since 1908.

Phenotyping
Phenotypic data collected for selected seedlings in 2014 and 2015 included plant yield, fruit weight, fruit diameter, fruit firmness, and fruit stem diameter. Yield was measured using a 1-to-5 rating scale, where 1 equaled none to very few berries on the plant and 5 equaled a yield comparable with commercial cultivars of the same age plant. Yield ratings were recorded over a 2-wk period before the blueberries were fully mature.

Fruit traits were determined using five randomly sampled representative berries from each genotype. Because of the diversity of harvest timing among the individual selections, the berries were collected over a 6-wk period from the beginning of April to the middle of May in each year. The total sample of berries was hand harvested from each genotype when they were fully mature and had no insect or visual damage. After harvest, the berries were kept in a cooler and stored at 4°C overnight prior to analysis. Weight (g) was measured on each individual berry using an analytical scale (CP2202S, Sartorius Corp.). The same five berries were oriented equatorially for fruit size diameter (mm) and firmness (g mm⁻¹ compression force) measurement using a FirmTech II (BioWorks Inc.). The minimum and maximum force thresholds were set at 50 g and 350 g, respectively.

Subsequently, each of the berries was placed with the stem scar positioned upward on a tray in a light box with a digital SLR (Pentax K-x, Ricoh Imaging) camera positioned 50 cm above the berries. The camera was set at a shutter speed of 1/50, aperture F 5.6, and ISO 200. A ruler was placed in each image as a size reference. Subsequently, the images were uploaded into FIJI (Schindelin et al., 2012) and the scale was set using the ruler. Scarc diameter (mm) was measured and recorded for each fruit. The average weight (g), diameter (mm), firmness (g mm⁻¹), and scar diameter (mm) of the five berries was calculated and used for subsequent analyses.

Analysis and Model Comparison
Variance components were estimated with REML and BVs with BLUP using ASReml version 3.0 (Gilmour et al., 2009) with the following univariate linear mixed models:

\[
y = I_n \mu + Xb + Z_c c + Z_r r + Z_g a + Z_e e + a + e
\]

where \(y\) is a vector of the trait being analyzed (i.e., yield, weight, firmness, diameter, or scar), \(I_n\) is a vector of ones, \(\mu\) is the overall mean, \(b\) is the fixed effect of year, \(c\) is the random effect of column nested within year \(\sim N(0, \sigma^2_c)\), \(r\) is the random effect of row nested within year \(\sim N(0, \sigma^2_r)\), \(a\) is the random effect of genotype \(\sim N(0, \sigma^2_a)\), \(b \times a\) is the random effect of the interaction of year \times\) genotype \(\sim N(0, \sigma^2_{b \times a})\), \(c\) is the random residual effect \(\sim N(0, \sigma^2_c)\), \(X\), \(Z_c\), and \(Z_r\) are incidence matrices for year, column, row, genotype and year \times\) genotype interaction, respectively. The unbiased heritability was calculated as

\[
h^2 = \sigma^2_g / (\sigma^2_g + \sigma^2_c + \sigma^2_r + \sigma^2_{b \times a} + \sigma^2_e)
\]

The A matrix was constructed with the AGHMatrix R package as described below.

Matrix Construction with AGHMatrix
To build the pedigree-based relationship matrices, we constructed an R package named AGHMatrix. The package is freely available for download at https://github.com/prmunoz/AGHMatrix. To build the relationship matrix derived from the pedigree using the AGHMatrix package, the pedigree information needs to be formatted in three columns (individual, Parent 1, and Parent 2) and read as a table in R (using read.table or read.csv functions). The pedigree file should be sorted from older to newer generations, thus the oldest generation (founders) without pedigree information should appear at the top of the file, while the current generation being phenotyped is at the bottom of the file. Before proceeding to build the relationship matrix, the AGHMatrix verifies that the above order is correct, and if not, it will flag and permute the order of misplaced individuals. More details of the package’s functions can be found in the manual at https://github.com/prmunoz/AGHMatrix/blob/master/vignettes/tutorial.pdf.

The autotetraploid pedigree-based relationship matrix \(A_w\) was calculated as presented in Slater et al. (2013). The algorithm first computes the matrix \(K\)
considering the proportion of parental gametes that are identity by descent as a result of double reduction w. Thus for every individual k, with parents s and d,

If s and d of a_i are unknown, they are assumed unrelated, and

\[ k_{ij} = k_{ji} = 0; \text{for } j = 1:(i - 1) \]
\[ k_{ij} = (1 + w)/4 \]

If only s is known, d is assumed nonrelated, and

\[ k_{ij} = k_{ji} = 0.5(k_{j} + k_{j}); \text{for } j = 1:(i - 1) \]
\[ k_{ii} = [5 + 7w + 4k_s(1 - w)]/24 \]

If s and j are known, then

\[ k_{ij} = k_{ji} = 0.5(k_{j} + k_{j}); \text{for } j = 1:(i - 1) \]
\[ k_{ii} = [1 + 2w + (1 - w)k_{ss} + (1 - w)k_{sd} + 3k_{dd}]/6 \]

Finally, the matrix A_w is given by A_w = 4K. Six A_w matrices were constructed from the pedigree assuming varying levels of double reduction (w): 0, 0.05, 0.10, 0.15, 0.20, and 0.25. Additionally, we also built the traditional diploid pedigree-based relationship matrix (A-matrix) using the AGHmatrix R package, which is calculated according to the recursive method presented in Mrode (2014) and described by Henderson (1976). The AGHmatrix R package can also build the genomic-base relationship matrix, G-matrix, for diploids using either the method proposed by VanRaden (2008) or from Powell et al. (2010). To calculate the G-matrix, molecular data needs to be in table format where n is the number of individuals (in rows) and m is the number of loci (in columns). The loci information is set to –1, 0, 1, for the genotypes aa, Aa, and AA, respectively. Although the G-matrix capability is present in the package, the genomic matrix was not built or used in this study.

The autotetraploid matrices with different levels of double reduction were used in the linear mixed model described above. These autotetraploid models were compared against the diploid counterpart using the Akaike information criteria (AIC). As the level of double reduction w is unknown, we inferred its level based on the model that maximized the likelihood of the data given the parameters of the linear mixed model.

Results and Discussion

Using AGHmatrix to Determine Trait-Specific Levels of Double Reduction

A unique challenge to plant breeders dealing with autotetraploid potato found that the model best estimating the proportion of double reduction varied between 0 and 0.25 depending on the trait considered (Slater et al., 2013). Double reduction is expected to differ from trait to trait because it is a position-dependent phenomenon.
fluctuating between chromosomes based on the frequency of multivalent formation and within chromosomes depending on where the measured loci reside (Wu et al., 2001). Bourke et al. (2015) found a parallel increase between the rate of double reduction and the distance from the centromere using a high-density set of markers in autotetraploid potato. The rate of double reduction increases toward telomeres because there is a greater probability of a crossover to occur between the centromere and the loci (Bourke et al., 2015; Luo et al., 2006; Welch, 1962; Wu et al., 2001). The high proportion of double reduction for firmness suggests that genes controlling this trait may reside toward the distal end of a chromosome. Thus, in the same line, the genes controlling yield, weight, diameter, and scar may be located closer to the centromere, be quantitative in nature and dispersed over the whole genome, or located on chromosomes that do not exhibit much multivalent formation.

Impact of Increasing Double Reduction Levels on Heritability and Relationship Estimates

Heritability estimations were not significantly different when assuming tetrasomic inheritance with zero double reduction ($w = 0$) instead of disomic inheritance for all traits (Table 1). However, firmness was the only trait that showed a better fit with the tetrasomic model considering higher levels of double reduction, thus the heritability for the tetrasomic model was estimated using $w = 0.15$, which was the level of double reduction that fit the data best (Table 1).

The heritabilities estimates for firmness had the largest difference between the two models, decreasing from 0.40 to 0.35 as a result of the larger proportion of double reduction used in the estimation. As seen in Fig. 2, there

Table 1. The heritability of five breeding traits calculated assuming disomic and tetrasomic inheritance. Tetrasomic inheritance was estimated assuming no double reduction for all traits except firmness where 0.15 was used.

<table>
<thead>
<tr>
<th>Trait</th>
<th>Disomic inheritance</th>
<th>Tetrasomic inheritance</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Heritability</td>
<td>Standard error</td>
</tr>
<tr>
<td>Yield</td>
<td>0.46</td>
<td>0.02</td>
</tr>
<tr>
<td>Weight</td>
<td>0.58</td>
<td>0.02</td>
</tr>
<tr>
<td>Firmness†</td>
<td>0.40</td>
<td>0.03</td>
</tr>
<tr>
<td>Fruit diameter</td>
<td>0.26</td>
<td>0.03</td>
</tr>
<tr>
<td>Scar diameter</td>
<td>0.54</td>
<td>0.02</td>
</tr>
</tbody>
</table>

† Tetrasomic inheritance was calculated assuming double reduction of 0.15.
is a small difference between the disomic-estimated heritability for firmness and the tetrasomic-estimated heritability with no double reduction. The difference becomes more pronounced, and the narrow-sense heritability for the trait decreases as the proportion of double reduction increases. This trend was seen in all the traits measured (data not shown). Comparing disomic and tetrasomic inheritance with \( w = 0.10 \) in autotetraploid potatoes, Slater et al. (2013) observed no consistent trend and found the difference in heritability ranged from 0.01 to 0.13 depending on the trait being analyzed.

The downward trend in heritability observed for blueberry fruit firmness can be explained by the increased inbreeding caused by increasing the levels of double reduction. As double reduction increased, the kinship coefficient also increased (Table 2). The maximum coefficient was determined by the amount of double reduction, whereas the minimum kinship coefficient was unaltered by the level of double reduction. A large number of the individuals in the pedigree had unknown ancestry, which negatively skewed the distribution. Unknown ancestry was a result of missing information, unspecified clones, and wild selections. These individuals were assumed to be unrelated and thus unaffected by double reduction. As double reduction increased the kinship coefficient increased as well. This can be seen by comparing the kinship coefficients obtained for \( w = 0 \) and those obtained for \( w = 0.25 \) (Table 2). The effects of double reduction are cumulative with larger kinship coefficients more susceptible to its effects. In the first quartile, the difference between the kinship coefficients estimated assuming \( w = 0 \) and the coefficient estimated assuming \( w = 0.25 \) was 0.021, while this difference almost doubles (0.046) in the third quartile.

The BLUP analysis uses these kinship coefficients and estimations of heritability to predict BVs. Thus, inaccurate estimations of double reduction could lead to bias predictions. Higher relationships should suffer a larger impact as these are more affected by double reduction.

### Table 2. Average of the relationship coefficient between two individuals assuming various levels of double reduction.

<table>
<thead>
<tr>
<th>Double Reduction</th>
<th>Min.</th>
<th>First quartile</th>
<th>Median</th>
<th>Mean</th>
<th>Third quartile</th>
<th>Max.</th>
</tr>
</thead>
<tbody>
<tr>
<td>0</td>
<td>0</td>
<td>0.067</td>
<td>0.106</td>
<td>0.115</td>
<td>0.148</td>
<td>1.000</td>
</tr>
<tr>
<td>0.05</td>
<td>0</td>
<td>0.071</td>
<td>0.113</td>
<td>0.123</td>
<td>0.158</td>
<td>1.050</td>
</tr>
<tr>
<td>0.10</td>
<td>0</td>
<td>0.076</td>
<td>0.120</td>
<td>0.130</td>
<td>0.168</td>
<td>1.100</td>
</tr>
<tr>
<td>0.15</td>
<td>0</td>
<td>0.080</td>
<td>0.126</td>
<td>0.138</td>
<td>0.177</td>
<td>1.150</td>
</tr>
<tr>
<td>0.20</td>
<td>0</td>
<td>0.084</td>
<td>0.133</td>
<td>0.145</td>
<td>0.186</td>
<td>1.200</td>
</tr>
<tr>
<td>0.25</td>
<td>0</td>
<td>0.088</td>
<td>0.139</td>
<td>0.151</td>
<td>0.194</td>
<td>1.250</td>
</tr>
</tbody>
</table>

Fig. 2. The estimated narrow-sense heritability for firmness assuming disomic inheritance and tetrasomic inheritance with increasing coefficients of double reduction.
Nevertheless, there was a strong correlation ($r = 0.999$) between the diploid and tetraploid ($w = 0.15$) estimated BVs for firmness (Fig. 3). This strong correlation was seen for all traits when analyzed with tetraploid models assuming $w = 0$ (data not shown). Similarly, Slater et al. (2013) found a strong correlation ($>0.95$) for eight of the nine traits when comparing the diploid estimated BVs with the autotetraploid estimated BVs. The depth of the pedigree could help balance and compensate erroneous estimations, resulting in small changes to the BVs over various levels of double reduction. In this case, the pedigree covered the whole breeding program beginning with its origin in 1908.

**Effect of Pedigree Depth on Double Reduction Estimate**

In the example data set we have used, there is an extensive pedigree available beginning with known founder clones dating back to 1908 (Coville, 1937). However, the detail of pedigree information available for blueberry may not be available for other autotetraploid plant breeders. To study the consequences of using truncated or incomplete pedigree information while studying double reduction using these methods, we truncated the pedigree to 5, 10, 20, and 30 yr (back to 2009, 2004, 1994, and 1984, respectively).

Different levels of double reduction maximize the fitting of the data when using different pedigree depths (Fig. 4). By using only 5 yr of data (back to 2009) the level of double reduction is estimated to be the maximum coefficient tested in this study, 0.25, for four out of five traits, and 0.20 for the last trait. In this case, all the traits had the worst fit assuming no double reduction. When 10 yr of pedigree information was used, three traits followed the same pattern as when using 5 yr of pedigree information, no double reduction was estimated for one trait, while the fit for the final trait was maximized at a double reduction level of 0.05. As more pedigree information was added, the slopes continued to change, but even when 30 yr of pedigree information were used, it was not enough to observe the estimation of double reduction seen when all the pedigree information was used. Thus, shallow pedigrees underestimate the actual kinship coefficient between two individuals. For example Boyce (1983) found that shallow pedigrees miscalculate the level of inbreeding when analyzing 10 Standardbred stallions with 30 generations worth of pedigree information. In blueberries, there has been a steady increase in inbreeding with each consecutive generation as a result of recurrent selection (Brevis et al., 2008; Hancock and Siefker, 1982; Ehlenfeldt, 1994). Relationships are further intensified by the narrow gene pool created in the founding event. Based on pedigree information, Ehlenfeldt (1994) concluded that three cultivars, Brooks, Sooy, and Rubel, have contributed the largest portion of genes in

![Fig. 3. Correlation of breeding values for firmness estimated assuming disomic and tetrasomic inheritance with $w = 0.15$.](image-url)
79 highbush cultivars (23.5, 12.5, and 28.6%, respectively) and _V. darrowi_ contributions can be traced back to germplasm sources Florida 4B, Florida 4A, Florida 9A, and clone D (Brevis et al., 2008). The limited pedigree information cannot accurately account for these intertwined relationships. Thus, the higher proportions of double reduction compensated for the lack of information by increasing the assumed relationships between the individuals and thus better fitted the model. Atkin et al. (2009) and Mehrabani-Yeganeh et al. (1999) found the accuracy of estimating additive variance components and BVs improved when using more pedigree information. Atkin et al. (2009) discovered that the variances were estimated with the same precision once five generations were used, suggesting older generations do not contribute much information to the model. This is mainly because the coefficients of relationships with the current population become smaller as generation distance increases. However, using shallow pedigrees can lead the erroneous conclusions in the estimation of relationship coefficients and thus incorrect determination of the level of double reduction for each trait. This will also impact the estimated heritability, inbreeding, and BVs.

**Conclusion**

We have developed an R package, AGHmatrix, that can be used to quickly develop relationship matrices for autotetraploid crop species. To illustrate the utility of this package, we used the pedigree and phenotypic data from a blueberry breeding program. The majority of traits (yield, weight, diameter, and scar) had the best fit assuming tetrasomic inheritance with no double reduction. The only exception was firmness, which had the best fit when double reduction was 0.15. Changes in the estimation of heritability occurred with larger proportions of double reduction. However, there was no significant improvement in BV estimates for the blueberry traits assessed when comparing tetrasomic inheritance accounting for the correct levels of double reduction with...
a simple disomic inheritance model. The effects of double reduction are cumulative, and shallow pedigree depths can underestimate the true kinship coefficient and, as a result, report inflated levels of double reduction, which can affect the estimation of the genetic parameters. As double reduction is trait dependent, this package should allow autotetraploid breeders to estimate the levels of double reduction and how it affects genetic parameters and ultimately breeding progress.

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