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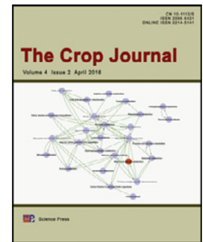

Estimation of genetic parameters and their sampling variances for quantitative traits in the type 2 modified augmented design

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ABSTRACT

The type 2 modified augmented design (MAD2) is an efficient unreplicated experimental design used for evaluating large numbers of lines in plant breeding and for assessing genetic variation in a population. Statistical methods and data adjustment for soil heterogeneity have been previously described for this design. In the absence of replicated test genotypes in MAD2, their total variance cannot be partitioned into genetic and error components as required to estimate heritability and genetic correlation of quantitative traits, the two conventional genetic parameters used for breeding selection. We propose a method of estimating the error variance of unreplicated genotypes that uses replicated controls, and then of estimating the genetic parameters. Using the Delta method, we also derived formulas for estimating the sampling variances of the genetic parameters. Computer simulations indicated that the proposed method for estimating genetic parameters and their sampling variances was feasible and the reliability of the estimates was positively associated with the level of heritability of the trait. A case study of estimating the genetic parameters of three quantitative traits, iodine value, oil content, and linolenic acid content, in a biparental recombinant inbred line population of flax with 243 individuals, was conducted using our statistical models. A joint analysis of data over multiple years and sites was suggested for genetic parameter estimation. A pipeline module using SAS and Perl was developed to facilitate data analysis and appended to the previously developed MAD data analysis pipeline (http://probes.pw.usda.gov/bioinformatics_ tools/MADPipeline/index.html).

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1. Introduction

In the early stages of breeding programs, a considerable number of test lines and a limited seed supply constrain the use of complete experimental designs with replications. Augmented designs, a class of unreplicated experimental designs, are a potential solution to this problem [1–3]. The augmented design usually has control lines arranged in a standard design such as a Latin square with several replications in soil-homogeneous blocks. Then the blocks are augmented to accommodate unreplicated test lines. Since control lines are in a standard design, the block effects can be estimated to adjust the observations of the test lines, and the error effects within control lines can be used to test the significance of performance differences among lines. Lin and Poushinsky [4,5] proposed a modified augmented design (MAD) with two subtypes. The type 1 MAD is used for square plots [4] and the type 2 MAD (MAD2) for rectangular plots [5]. This modified design is superior to the general augmented design in systematic placement of control and test genotypes within a block to enhance adjustment for soil heterogeneity [4].

MAD2 is used largely for early evaluation of breeding lines in crops such as wheat [6,7], potato [8], soybean [9], barley [10,11], sugarcane [12,13], and maize [14]. It is also used in flax breeding programs in Canada for field evaluation of flax yield, seed oil component, disease resistance, and other traits of agronomic and economic importance and for purposes of QTL identification, association mapping, and genomic selection [15–18]. In genetic experiments, individuals may have adequate amounts of seed for replicated trials, but it may be impractical to accommodate hundreds of genotypes in one homogeneous block of a field, owing to soil heterogeneity. Our earlier study [19] indicated that soil heterogeneity can be sufficiently adjusted for traits in MAD2 trials, suggesting that genetic variance of traits can be determined using a MAD2 approach.

Heritability and genetic correlation are crucial genetic parameters for quantitative traits because they can be used to predict the response to selection in plant breeding. Because the theoretical statistical distributions of these genetic parameter estimators are unknown, approximate tests of significance can be performed only on the basis of sampling errors. Methods for estimating sampling variances of the genetic correlation coefficient and heritability in some replicated experimental designs have been reported [20–24].

We have improved upon previous methods of MAD2 statistical analysis in adjusting for soil heterogeneity [19]. Owing to the lack of replication of test genotypes in the design, however, the total variance for test genotypes cannot be partitioned into its genetic and error components, and for this reason the method is unable to estimate genetic parameters. Here we present a method for estimating broad-sense heritability (H^2) and genetic correlation coefficients (r_g) of quantitative traits in the MAD2. We also derive the statistical formulas for estimating their sampling variances. We used computer simulations to evaluate the reliability of the proposed methods. As a case study using flax, we estimated the genetic parameters of three quantitative traits in a biparental recombinant inbred line (RIL) population of 243 lines.

2. Methods

2.1. Experimental design and statistical analysis

A typical MAD2 has $r * c$ whole plots structured as a grid of r rows and c columns. Each whole plot is split into k (an odd number, usually five or seven) parallel rectangular subplots. The whole experiment has a total of $r * c * k$ subplots. A control genotype is assigned to the central subplot of each whole plot (plot control). Two additional control genotypes serve as subplot controls randomly assigned to subplots in randomly selected whole plots with n replicates. Thus, the entire trial accommodates $rck - rc - 2n$ test genotypes that are randomly allocated to the remaining subplots (see Fig. 1 in [19] for the field layout).

Control plots are used to estimate row (R), column (C) and R × C interaction effects and to test for additive soil variation in the row and/or column directions. The two subplot controls plus one plot control are used to estimate the subplot error and test for non-additive soil variation in multiple directions across the field [9,19]. The test results are used to determine whether data adjustment is needed and which method of adjustment should be used. Three methods have been proposed to adjust test genotypes to reduce or remove effects due to soil heterogeneity [4,5,9]. For MAD2, method 1 is used if the row or column effects or both are significant, method 3 is used if the R × C interaction is significant [5,9,25] and a combined methods 1 and 3 approach is suggested in most cases [19]. A detailed statistical analysis for MAD2 trials has been described [19].

2.2. Case study

An RIL population with 243 lines derived from a cross between “CDC Bethune” and “Macbeth” (BM) was used to evaluate genetic variation. The single MAD2 trial consisted of 49 whole plots (7 × 7 grids), each splits into seven parallel subplots (1.5 m × 2.0 m with a 20-cm row spacing). CDC Bethune with 49 replicates was used as the plot control, and 7 replicates of both Hanley and Macbeth served as subplot controls. Field trials with the same design were conducted at two locations in Canada (Morden, Manitoba and Kernen Farm near Saskatoon, Saskatchewan) from 2009 to 2012 [18]. Genetic parameters and their sampling variances were estimated for three traits: oil content (OIL), iodine value (IOD), and linolenic acid content (LIN). The raw phenotypic data are presented in Table S1.

2.3. Estimation of genetic parameters

Observations of test genotypes and control genotypes after statistical adjustment [19] are expected to exclude the effect of soil heterogeneity; thus, the variation among replications of each control genotype should be caused only by random errors. The adjusted dataset in the trials corresponds to that obtained from a completely random design. Because each test genotype has a single adjusted observation, the total variance among test genotypes cannot be partitioned into genetic and error variances. However, the total variance within each control genotype, which is caused by random error, can be treated as the error variance of the test genotypes because it is reasonable to assume that any

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