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Analysis on genetic contribution of agronomic traits to total sugar in flue-cured tobacco (*Nicotiana tabacum* L.)

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Abstract

To uncover the genetic contributions of agronomic traits to content of total sugar (TS) and find indicator traits for indirect selection on TS in the flue-cured tobacco (*Nicotiana tobacum* L.), multivariable conditional analysis was conducted based on a genetic model containing additive–dominance and their interactions with environments. Fourteen cultivars (or breeding lines) and derived 41 F_1 crosses were grown at four locations in Yunnan province, China. Significant phenotypic contribution to TS was detected for six agronomic traits, plant height (PH), girth of stem (GS), internode length (INL), number of leaves (NL), length of middle leaves (LML) and width of middle leaves (WML). There was large contribution of additive effects due to each of the five agronomic traits (PH, GS, INL, LML and WML). The contribution ratio of dominance effect was high due to PH. By serving as high contributor of additive effects to TS and having high ratios of additive variance to phenotypic variance, INL and PH could be used as indicative agronomic traits for selecting breeding lines with suitable TS. Among the six agronomic traits, PH had the highest contribution to dominance effects of TS for most F_1 crosses, and could be used for selecting the crosses with suitable TS.

Keywords: Flue-cured tobacco; *Nicotiana tobacum* L.; Diallel analysis; Genetic correlation; Conditional analysis

1. Introduction

The flue-cured tobacco (*Nicotiana tabacum* L.) is one of the most commercially valued crops. The major goal in flue-cured tobacco breeding is to develop cultivars with acceptable cured leaf quality. As the decisive factors influencing leaf quality, the chemical constituents of leaves, such as total sugars and nicotine, determine the taste, flavor, and aroma in cigarettes (Pandeya et al., 1985). There are few clues on the chemical components of leaves before they were harvested and cured. It will be helpful to tobacco breeders in the indirect selection on chemical constituents of leaves by the information on the genetic association between chemical constituents and visible and detectable agronomic traits, for example, plant height, number of leaves, length and width of leaves.

Correlation analysis has been conducted among agronomic traits (Legg et al., 1965; White et al., 1979; Pandeya et al., 1983; Lalitha and Atluri, 2002), among chemical constituents (Legg et al., 1965; White et al., 1979; Pandeya et al., 1985) and between chemical constituents and agronomic traits (Legg et al., 1965; White et al., 1979) in the flue-cured tobacco. However, the correlation coefficients are measures of concomitant variation of various characteristics (White et al., 1979) and could not be used to evaluate the actual contribution of one agronomic trait to certain chemical constituents of leaves.

Path analysis (Wright, 1921) permits the separation of the correlation coefficient into direct effects and indirect effects and has been used by plant breeders to assist in identifying traits that are useful as selection criteria to improve crop yield (Kang et al., 1983; Gravois and McNew, 1993; Agrama, 1996; Sarawgi et al., 1997; Samonte et al., 1998; Wang et al., 1999; Board et al., 1999; Mohammadi et al., 2003). Since path coefficient is the standardized partial regression coefficient, its value can vary according to the other variables. In addition, this approach might result in multicollinearity for variables, particularly when component traits are highly correlated (Samonte et al., 1998).

A conditional approach has been developed (Zhu, 1995) and used for studying the developmental behavior of quantitative

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traits in several crops (Zhu, 1995; Shi et al., 2001, 2002; Ye et al., 2003). By analysis of conditional variance components and conditional genetic effects, this method can also be used for evaluating extra genetic variation and gene effects of target trait conditional on any one of given variables (Zhu, 1995; Atchley and Zhu, 1997). The objectives of this study were to ascertain genetic contribution of agronomic traits to the content of total sugars (TS) by multivariable conditional analysis and find key indicator of agronomic traits influencing TS in the flue-cured tobacco, which may be useful in indirect selection for breeding high quality cultivars with suitable TS.

2. Materials and methods

Fourteen flue-cured tobacco cultivars (or breeding lines) were used as the parents for constructing diallel matting of 41 F_1 crosses. Eight cultivars, K326, Yunnan tobacco No. 85 (YT85), NC89, Red flower mammoth golden (RF Golden), NC82, Speight G-28 (G-28), K358 and Yunnan tobacco No. 317 (YT317), were grown commercially and represented over 90% of the flue-cured tobacco acreage in China. Coker176, SC71 and pure yellow leaf (pure YL) were often used as parents resistant to TMV, CMV and brown spot disease, respectively. Three breeding lines, Line41, C2, and 96-19, were included in this study because of their various special characteristics to a cross.

The 14 parent lines and their 41 F_1 crosses were evaluated in 2002 at four locations represented different ecologic environments in Yunnan, southern west of China. At each location, genetic entries were arranged by a randomized complete block design with two replications. Each plot consisted of 18 parent or F_1 plants on a single 9.0 m row which were 1.2 m apart. Plant spacing was 0.5 m. Normal cultural and production practices for the flue-cured tobacco were followed throughout the field evaluation, curing and grading. The agronomic traits measured were plant height (PH, cm), girth of stem (GS, mm), internode length (INL, mm), number of leaves (NL, No.), length of middle leaves (LML, cm), and width of middle leaves (WML, cm). The data of agronomic traits were collected from five competitive plants in each plot for generating mean values. The content of total sugar (TS, %) were evaluated on the cured leaves. A 50-g cured leaf composite sample from the middle leaves for each plot was ground for determination of TS.

The data were analyzed using a genetic model including additive–dominance effects and their interactions with environments. The phenotypic value of a trait for the F_1 cross between parent i and j or for parent i (when $i = j$) in the kth block within environment h can be partitioned as

$$y_{hijk} = \mu + E_h + A_i + A_j + D_{ij} + AE_{hi} + AE_{hj} + DE_{hij} + B_{k(h)} + e_{hijk}$$

where μ is the population mean, E_h the environment effect, A_i or A_j is the additive effect, D_{ij} the dominance effect, AE_{hi} or AE_{ji} the additive × environment interaction effect, DE_{hij} the dominance × environment interaction effect, $B_{K(h)}$ the block effect, and, e_{hijk} is the residual effect.

The variances of random effects were estimated by MINQUE(1) method (Zhu and Weir, 1996). An adjusted unbiased prediction (AUP) method (Zhu, 1993; Zhu and Weir, 1996) was used for predicting the random genetic effects. The phenotypic variance ($V_P = V_A + V_D + V_{AE} + V_{DE} + V_e$) or covariance ($C_P = C_A + C_D + C_{AE} + C_{DE} + C_e$) can be partitioned into five components, which can be further used in calculating correlation between two traits for phenotypic correlation ($r_P = C_P/\sqrt{V_{P(1)}V_{P(2)}}$), additive genetic correlation ($r_A = C_A/\sqrt{V_{A(1)}V_{A(2)}}$), dominance genetic correlation ($r_D = C_D/\sqrt{V_{D(1)}V_{D(2)}}$), additive × environment interaction genetic correlation ($r_{AE} = C_{AE}/\sqrt{V_{AE(1)}V_{AE(2)}}$), and dominance × environment interaction genetic correlation $\left(r_{DE} = C_{DE}/\sqrt{V_{DE(1)}V_{DE(2)}}\right)$.

Conditional random variables of $\boldsymbol{y}_{(T)}/\boldsymbol{y}_{(C)}$ for the target trait $\boldsymbol{y}_{(T)}$ conditional upon the phenotypic mean of component trait $\boldsymbol{y}_{(C)}$ can be obtained by mixed model approaches (Zhu, 1995; Atchley and Zhu, 1997) for further calculating conditional variance components ($V_{(T/C)}$) and conditional genetic effects $G_{(T/C)}$. The proportion of $V_{(T/C)}/V_{(T)}$ can uncover the contribution of genetic variances without the influence of the given component trait $\boldsymbol{y}_{(C)}$ on the target trait $\boldsymbol{y}_{(T)}$, and contribution ratio $CR_{u(C\to T)} = 1.0 - \sigma^2_{u(T/C)}/\sigma^2_{u(T)}$ could be used for measuring the contribution proportion of genetic variances of the given component trait $\boldsymbol{y}_{(C)}$ on the target trait $\boldsymbol{y}_{(T)}$. Contributed effects $G_{(C\to T)} = G_{(T)-(T/C)}$ could be used for measuring genetic effects of the given component trait $\boldsymbol{y}_{(C)}$ on the target trait $\boldsymbol{y}_{(T)}$.

Jackknifing over genotypes was used to estimate standard errors of estimated genetic variances and correlation coefficients (Zhu and Weir, 1996). All statistical analysis was conducted by QGAStation software (http://ibi.zju.edu.cn/software/QGA.htm).

3. Results

3.1. Variance components for agronomic traits and TS

The estimated phenotypic variance and genetic variance components were presented in Table 1 for six agronomic traits and TS. The genetic variance components (V_A, V_D, V_{AE}, V_{DE}, and V_ε) were significant for all the traits studied. It was suggested that the six agronomic traits, PH, GS, INL, NL, LML and WML and TS were controlled by genetic main effects (additive and dominance) as well as genotype × environment interaction effects. It was indicated, by high ratios of additive genetic variance to phenotypic variance (V_A/V_P) for PH (0.423) and INL (0.442), that the selection in early generation could obtain apparent genetic gain for PH and INL. Large proportion of dominance × environment interaction variance (V_{DE}/V_P) for GS (0.322), NL (0.279), LML (0.322) and TS (0.223) indicated that utilization of heterosis could be feasible in special environments. The fact that the ratio of residual variance to phenotypic variance (V_e/V_P) for TS (0.436) was higher than those for agronomic traits (0.320 for PH, 0.249 for GS, 0.338 for INL, 0.346 for NL, 0.321 for LML and 0.310 for WML) suggested that TS was more sensitive to measuring variation and sampling errors than agronomic traits.