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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.
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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

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.

Table 1
Estimated phenotypic variance and genetic variance components for six agronomic traits and TS in the flue-cured tobacco

Parameters	PH	GS	INL	NL	LML	WML	TS
V_P[a]	145.398[**]	103.566[**]	62.182[**]	1.571[**]	11.995[**]	6.579[**]	7.898[**]
V_A[b]	61.548[**]	12.217[**]	27.495[**]	0.284[**]	2.113[**]	2.052[**]	0.918[**]
V_D[c]	13.627[**]	3.925[**]	9.069[**]	0.191[**]	1.739[**]	0.729[**]	0.704[**]
V_{AE}[d]	6.799[**]	28.330[**]	0.034[**]	0.114[**]	0.426[**]	0.444[**]	1.073[**]
V_{DE}[e]	16.842[**]	33.300[**]	4.574[**]	0.439[**]	3.868[**]	1.315[**]	1.762[**]
V_e[f]	46.583[**]	25.793[**]	21.009[**]	0.544[**]	3.850[**]	2.040[**]	3.442[**]

[a] Phenotypic variance.
[b] Additive variance.
[c] Dominance variance.
[d] Additive × environment interaction variance.
[e] Dominance × environment interaction variance.
[f] Residual variance.
[**] $P < 0.01$.

Table 2
Estimated correlation coefficients of genetics components between TS and agronomic traits in the flue-cured tobacco

Parameters	TS and PH	TS and GS	TS and INL	TS and NL	TS and LML	TS and WML
r_P[a]	0.127[**]	0.087[**]	0.129[**]	0.027	0.063[**]	0.076[**]
r_A[b]	0.352[**]	0.370[**]	0.454[**]	−0.136[**]	0.365[**]	0.330[**]
r_D[c]	0.159[**]	0.054[*]	0.108	−0.096[**]	0.112[**]	0.119[**]
r_{AE}[d]	0.159[**]	0.057[*]	0.000	0.065[*]	−0.116[**]	−0.075[**]
r_{DE}[e]	−0.052[*]	−0.026	0.000	0.151[**]	−0.055	0.059[**]

[a] Phenotypic correlation.
[b] Additive correlation.
[c] Dominance correlation.
[d] Additive × environment interaction correlation.
[e] Dominance × environment interaction correlation.
[*] $P < 0.05$.
[**] $P < 0.01$.

3.2. Correlation between agronomic traits and TS

Estimated correlation coefficients of genetic components between TS and agronomic traits in the flue-cured tobacco were presented in Table 2. There was significant positive phenotypic correlation (r_P) between TS and each of the five agronomic traits (PH, GS, INL, LML and WML). The additive correlation coefficients (r_A) were higher than other correlation coefficients. The dominance correlation coefficients (r_D) were closed to r_P for four traits (PH, GS, LML and WML). There was no high correlation between TS and five agronomic traits (PH, GS, INL, LML and WML) for r_{AE} and r_{DE}.

The cause of no significant phenotypic correlation between TS and NL was due to the fact of positive correlation for genetic main effects (r_A and r_D) but negative correlation for genotype × environment interaction effects (r_{AE} and r_{DE}) between these two traits.

3.3. Phenotypic and genetic contribution ratios of agronomic traits to TS

The phenotypic and genetic contribution ratios of six agronomic traits to TS were presented in Table 3. The phenotypic contribution ratios ($CR_{P(C \to T)}$) were significant for

Table 3
Estimated phenotypic and genetic contribution ratios of agronomic trait (C) to TS (T)

Parameters	PH (%)	GS (%)	INL (%)	NL (%)	LML (%)	WML (%)
$CR_{P(C \to T)}$[a]	11.2[**]	8.4[**]	10.1[**]	4.6[**]	7.8[**]	6.6[**]
$CR_{A(C \to T)}$[b]	42.8[**]	55.9[**]	69.8[**]	−2.8	42.0[**]	34.5[**]
$CR_{D(C \to T)}$[c]	41.7[**]	12.0[**]	17.2[**]	−0.2	15.3[**]	18.0[**]
$CR_{AE(C \to T)}$[d]	15.4[**]	2.0[**]	−0.1	29.9[**]	10.3[**]	2.5[**]
$CR_{DE(C \to T)}$[e]	−2.5	−3.4	−0.7	2.8[**]	−0.6	3.7[**]

[a] Phenotypic contribution ratios of C to T.
[b] Additive contribution ratios of C to T.
[c] Dominance contribution ratios of C to T.
[d] Additive × environment interaction contribution ratios of C to T.
[e] Dominant × environment interaction contribution ratios of C to T.
[**] $P < 0.01$.

all the six agronomic traits studied. It was revealed that the phenotypic variation of TS was significantly contributed by these agronomic traits. There was large contribution of additive effects due to each of five agronomic traits (PH, GS, INL, LML and WML), especially due to INL ($CR_{A(C \to T)}$ = 69.8%). It was suggested that genetic gain of indirect selection on the five traits was expectable in selecting superior lines for TS. There was no significant additive contribution of NL to TS. It meant that selection on NL could not result in apparent gain for TS. The dominance contribution ratio to TS was high for trait PH ($CR_{D(C \to T)}$ = 41.7%). It was indicated that improvement on TS of F_1 crosses could be realized by indirect selection on PH of F_1 crosses. It was suggested, by the fact of no dominance contribution of NL to TS, that the dominance effects of F_1 crosses for TS were not dependant on trait NL.

Although there was no significant contribution of genetic main effects of NL to TS, there was large contribution of additive × environment interaction ($CR_{AE(C \to T)}$) of NL to TS. It was implied that indirect selection on NL could obtain improvement for TS only in specific environments. Among the six agronomic traits, INL had the largest contribution to TS by additive effects ($CR_{A(C \to T)}$), but the smallest contribution by additive × environment interaction effects ($CR_{AE(C \to T)}$). It revealed that indirect selection on INL in various environments could obtain alike genetic gain on TS across environments. There were no apparently large contribution due to dominance × environment interaction effects ($CR_{DE(C \to T)}$) of agronomic traits to TS. It was suggested that there was no need for considering indirect selection in specific environments on the agronomic behavior of F_1 crosses.

3.4. Contributed additive effects of agronomic traits to TS

Predicted additive effects of TS (A_i) and contributed additive effects of six agronomic traits to TS ($A_{i(C \to T)}$) were presented in Table 4. There were significantly positive additive

effects of TS for four parents (Line41, RF Golden, YT85 and 96-19). For parents Line41 and RF Golden, the positive additive effects of TS resulted mainly from traits GS, INL and LML. For parent 96-19, the positive additive effect of TS was contributed mainly from PH, GS, INL and LML. Having large additive effect of TS and contributed positive additive effects of four agronomic traits (PH, GS, INL and WML) to TS, 96-19 could serve as a good parent in selection for inbred pure lines with high TS. For parent YT85, the contributed additive effects were small due to the six agronomic traits investigated, revealing less importance of additive effects of these traits contributed to TS.

There were negative additive effects of TS for parents Cocker176, NC89, K358 and Pure YL. The negative additive effects were mainly due to INL and WML for Coker176, INL and PH for NC89 and INL for K358. For parent Pure YL, the negative additive effect of TS resulted from negative contribution of five of the six agronomic traits except of NL. It was implied that Pure YL could be used as candidate parent to decrease TS of offspring.

There were no significant additive effects of TS for parents NC82, K326, YT317 and SC71. GS had negative contribution and LML had positive contribution to additive effects of TS for NC82. GS and INL had negative contribution and LML had positive contribution to additive effects of TS for K326. NL and WML had negative contribution and PH had positive contribution to additive effect of TS for YT317. LML had negative contribution and PH, INL and WML had positive contribution to additive effects of TS for YT317. Therefore, the insignificant additive effects of TS (A_i) might be resulted from the counteraction of contributive additive effects ($A_{i(C \to T)}$) due to various agronomic traits for these parents. There was also no significant additive effect of TS for C2. However, the six agronomic traits contributed significant negative additive effects to TS. It is possible that the other traits contributed positive additive effects to TS of C2.

Table 4
Predicted additive effects of TS (%) and contributed additive effects (%) of agronomic trait (C) to TS (T) for the parents in the flue-cured tobacco

Parents	A_i[a]	$A_{i(C \to T)}$[b]					
	TS	PH	GS	INL	NL	LML	WML
NC82	−0.101	−0.012[**]	−0.179[**]	−0.012[**]	0.013[**]	0.099[**]	0.037[**]
K326	0.114	−0.039[**]	−0.169[**]	−0.123[**]	−0.103[**]	0.185[**]	0.041[**]
Coker176	−0.551[**]	−0.102[**]	−0.063[**]	−0.272[**]	−0.088[**]	−0.109[**]	−0.230[**]
Line41	1.015[**]	0.232[**]	0.704[**]	0.523[**]	0.000	0.469[**]	0.203[**]
YT317	−0.070	0.281[**]	0.119[**]	0.056[**]	−0.124[**]	−0.034[**]	−0.121[**]
G-28	−0.330	−0.184[**]	−0.137[**]	−0.279[**]	−0.012[**]	−0.651[**]	0.029[**]
RF Golden	0.708[**]	0.129[**]	0.541[**]	0.425[**]	0.073[**]	0.557[**]	0.177[**]
NC89	−1.060[**]	−0.333[**]	−0.266[**]	−0.419[**]	0.067[**]	0.026[**]	−0.183[**]
SC71	−0.343	0.228[**]	−0.046[**]	0.179[**]	0.027[**]	−0.529[**]	0.311[**]
C2	−0.059	−0.424[**]	−0.206[**]	−0.413[**]	−0.100[**]	−0.002[**]	−0.018[**]
K358	−0.834[**]	−0.097[**]	−0.258[**]	−0.398[**]	−0.019[**]	−0.084[**]	−0.217[**]
Pure YL	−0.389[*]	−0.720[**]	−0.631[**]	−0.523[**]	0.242[**]	−0.460[**]	−0.553[**]
YT85	0.733[**]	0.108[**]	−0.169[**]	0.191[**]	0.008[**]	0.247[**]	−0.231[**]
96-19	1.168[**]	0.933[**]	0.760[**]	1.064[**]	0.016[**]	0.287[**]	0.755[**]

[a] Predicted additive effect of TS (T) for the ith parent.
[b] Contributed additive effects of C to T for the ith parent.
[*] $P < 0.05$.
[**] $P < 0.01$.

Table 5
Predicted dominance effects of TS (%) and contributed dominance effects (%) of agronomic trait (C) to TS (T) for F_1 crosses in the flue-cured tobacco

Crosses $P_i \times P_j$	D_{ij}[a]	$D_{ij(C \to T)}$[b]					
	TS	PH	GS	INL	NL	LML	WML
NC82 × NC89	−2.233[**]	−0.377[**]	−0.157[**]	0.164[**]	−0.065[**]	−0.248[**]	−0.126[**]
NC82 × K358	1.446[*]	0.440[**]	0.310[**]	0.038[**]	−0.025[**]	0.006[**]	−0.277[**]
K326 × C2	−1.702[**]	−0.614[**]	−0.430[**]	−0.436[**]	−0.116[**]	−0.096[**]	−0.284[**]
K326 × Pure YL	2.114[**]	0.609[**]	−0.201[**]	0.261[**]	0.135[**]	0.606[**]	0.528[**]
Line41 × Pure YL	−1.365[*]	−0.478[**]	−0.224[**]	−0.312[**]	0.135[**]	0.220[**]	−0.214[**]
K358 × YT85	−1.153[*]	−0.287[**]	−0.304[**]	−0.074[**]	0.070[**]	0.262[**]	0.061[**]

[a] Predicted dominant effect of TS (T) for the cross $P_i \times P_j$.
[b] Contributed dominant effects of C to T for the cross $P_i \times P_j$.
[*] $P < 0.05$.
[**] $P < 0.01$.

3.5. Contributed dominance effects of agronomic traits to TS

For six F_1 crosses with significant dominance effects of TS, the predicted dominance effects (D_{ij}) of TS and contributed dominance effects ($D_{ij(C \to T)}$) of six agronomic traits to TS were presented in Table 5. There were positive dominance effects of TS for NC82 × K358 and K326 × Pure YL. The positive dominance effect of TS was resulted mainly from traits PH and GS for NC82 × K358 and from traits PH, LML and WML for K326 × Pure YL. Having large dominance effect of TS and contributed positive dominance effects of five agronomic traits except GS to TS, K326 × Pure YL might be a promising cross with high TS.

There were negative dominance effects of TS for NC82 × NC89, K326 × C2, Line41 × Pure YL and K358 × YT85. Although there were significant negative contributions to dominance effects of TS due to five of six agronomic traits for NC82 × NC89, these agronomic traits were not the decisive traits which caused the highly negative dominance effects of TS, because of the low contributive dominance effects ($D_{ij(C \to T)}$). The negative dominance effects for K326 × C2 was resulted from the six agronomic traits, especially PH, GS and INL. The negative dominance effect was contributed from PH and INL for Line41 × Pure YL and PH and GS for K358 × YT85.

For five of the six crosses presented in Table 5, there were the highest contributed dominance effects due to PH among the six agronomic traits. For 16 of 35 crosses, which had no significant dominance effects of TS, PH had also the largest contribution to dominance effects of TS among the agronomic traits investigated. So it was feasible to select the crosses with suitable TS using PH as indicator trait.

4. Discussion

Conditional analysis was developed for analyzing conditional variance components and conditional genetic effects (Zhu, 1995; Atchley and Zhu, 1997). This method can be used for evaluating extra genetic variation and net genetic effects of target trait conditional on given variables. Therefore, the contribution of one agronomic trait to certain chemical constituent of leaves can be measured by conditional analysis. It can uncover not only the contributed genetic variance but also the contributed genetic effects for individual parent or F_1 cross due to agronomic traits.

When a given trait had large additive contribution ratio to the target trait, the given trait could be used as candidate trait in selecting parents or superior lines. Predicted additive effects of target trait and contributed additive effects of the given traits to target trait could provide information on choice of parents. The parents having large additive effects could be used to improve the performance of the off-springs. Since various parents have their own genetic and developmental characteristics, it is suggested that anyone of the given traits cannot contribute the highest additive effects to target trait for various parents. In breeding inbred lines, crosses should be made between parents of which additive effects of target trait are high and contributed additive effects of given traits are complementary. If a given trait had large dominance contribution ratio to the target trait, the given trait could be used as candidate trait for improving hybrid varieties. The F_1 crosses, for which most given traits contributed superior dominance effects to the target trait, were more promising.

The content of chemical constituents of leaves in the flue-cured tobacco was key factors affecting leaf quality. Information on relationship between agronomic traits and chemical constituents of leaves will be helpful for indirect selection to improving chemical constituents. Considerable efforts have been directed at correlation analysis between agronomic traits and chemical constituents. For example, White et al. (1979) reported that percent reducing sugar was negatively correlated with leaf number and average length of the three top leaves, and positively correlated with average width of the three top leaves. In the present study, TS had positive correlation with PH, GS, INL, LML and WML, and no correlation with NL for phenotypic and genetic effects. TS was positively correlated with PH, GS, INL, LML and WML, and negative correlation with NL for additive effects. Since the correlation coefficients only reveal the relationship between agronomic traits and chemical constituents but not the contribution of agronomic traits to chemical constituents, conditional analysis could provide further information for expected gain in target trait due to indirect selection of contributed trait.

In this study, there was large contribution of additive effects due to each of five agronomic traits, PH, GS, INL, LML and WML, especially INL. The contribution ratio of dominance effects was high due to PH. These results were comparable to the results from correlation analysis. PH, GS, INL and LML frequently served as high contributor of additive effects to TS and NL contributed small additive effects to TS for all parents. Having high ratios of additive genetic variance to phenotypic variance, INL and PH can be used for the indicative agronomic traits to select the parents with suitable TS. Line 96-19 can serve as one of candidate parents in breeding inbred pure lines. Among the six agronomic traits, PH had the highest contribution to dominance effects of TS for most F_1 crosses, and can be used for selecting the crosses with suitable TS. K326 × Pure YL is a promising cross.

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