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Allometrical growth of the quantitative characters of plants II. The inheritance of plant leaf shape and leaf size of tobacco

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Abstract. In this paper, six generation means of tobacco (*Nicotiana tobacum*) were used to study the genetic mechanism of leaf size and shape by the method of generation mean analysis. Four models were considered to establish a suitable one, namely: (1) a three-parameter genetic model (Model 1), (2) a six-parameter digenic interaction genetic model (Model 2), (3) a six-parameter synthetical genetic model (Model 3), and (4) a twelve-parameter synthetical genetic model (Model 4). The data collected from six generations measuring three leaf positions and six growth periods of tobacco leaf shape index and leaf area were used for analysis. The results showed that additive and dominant gene effects, epistasis, and their interactions with growth time (Model 4) are adequate to illustrate the inheritance of leaf shape. Elongated leaf type is dominant over oval leaf type; top leaf has more variability of leaf shape than middle and lower leaves; dominant effect is negative and more influential than additive effect; additive, dominant and digenic interaction effects may change during growth. The additive-dominant model (Model 1) may be used to illustrate the genetic mechanism of leaf size in the third or fourth growth period for different leaf positions. Additive gene is negative and important to the leaf area. Dominant effect either has positive or negative value depending upon the leaf position. Small leaf size is dominant in top and lower leaves, but large leaf size is dominant in the middle leaves. It is still difficult to resolve the genetic mechanism of leaf size by these models.

Keywords: Genetic analysis; Leaf shape; Leaf size; Quantitative character; Tobacco.

Introduction

The shape of a leaf depends on the growth rates of its different parts. Study of allometrical growth enables biologists to examine the growth gradients of an organism's character, and to understand its form, functions, and biological niche, as well as the evolutionary processes that led to its present form.

Adamson (1983) studied inheritance of rosette leaf type in *Hibiscus sabdariffa* and found that the shallowly incised, broad-lobed leaf type found in most edible rosettes is recessive to both the deeply incised narrowly lobed leaf types in the fiber-type rosette and an obscurely lobed (non-lobed) leaf type from a wild rosette. The narrowly lobed type is dominant over the non-lobed type. Monogenic inheritance is usually considered to govern leaf shape, but the existence of two-locus inheritance can not be ruled out.

Branch (1987) detected a single recessive gene responsible for the inheritance of a curly-leaf shape in peanut plants. No maternal or cytoplasmic effects were detected among progenies from reciprocal hybridization. Inheritance of leaf shape in both turnip and rape was investigated by Geltink (1983). A 3:1 segregation ratio in F_2 generation was obtained in the inheritance of leaf shape for both plants. In turnip, the entire leaf was mono or digenically dominant over cutleaf. In rape, the entire leaf was incompletely monogenically dominant over cutleaf.

Shopova and Jordanov (1990) investigated the inheritance of ear leaf area in maize and showed that both genotypes and environments had considerable effects on the growth period. High heterosis effect and overdominance were evident in the inheritance of ear leaf area. Dominant gene effect [d] played an important role in the genetic control of maize ear leaf formation. It increased the expression of the character.

Park et al. (1994) observed that the leaf areas of the first trifoliolate leaf of the F_1 were similar to those of the broad-leafed parent in common beans. Generation-means analysis indicated that additive, dominance, and epistatic gene inheritances control the characters. The joint-scaling test based on either an additive-dominance (three-parameter) model or the additive-dominance interaction (six-parameter) model was not adequate. Low narrow-sense heritability was estimated for leaf size.

Achillea lanulosa has complex, highly dissected leaves that vary in shape and size along an altitudinal gradient. Gurevitch (1992) studied the sources of variation in leaf shape among two populations of this plant, concluding that there were genetic differences among populations and among individuals within populations in leaf size and shape. Leaves of the lower altitude population were larger and differed from the higher altitude plants in two types of leaf shape. Differences in leaf dissection and size at contrasting altitudes in this species are the result of both genetic divergence among populations and acclimative responses to local environments.

Wu (1994) developed a method to measure the changes of size and shape of leaves throughout the life of a plant,

using photographs and a digital tablet. He also developed a method for estimating leaf shape by constructing a linear function of allometrical growth between leaf length and width.

In this study, different models were used to analyze the inheritances of leaf sizes and leaf shapes of two different tobacco varieties. The relationship between genetics and environments was discussed.

Materials and Methods

Materials

Two cultivated tobaccos (*Nicotiana tobacum*) with dissimilar leaf shapes and sizes were selected as test subjects: Turkish var. Samsum 15A (P_1, small elongated leaf), native fluecurred tobacco var. TT5 (P_2, wide oval leaf), and their progeny F_1, F_2, B_1 as well as B_2. Ten plants of P_1, P_2 and F_1, 50 plants of B_1 and B_2, and 100 plants of F_2 were planted at the farm of the Taiwan Tobacco Research Institute. Photographs were taken every two or three days for three different layers of leaves, the lower, middle, and top. Five to six stages during the growth of each leaf were measured (Wu, 1994).

Methods

The width, length, and area of a photographic image of a leaf were measured with a digital tablet and the DGL software package on an HP 1000 computer. The leaf size and allometrical coefficient between leaf length and width for six generations were used to study the genetic mechanism of leaf size and shape (Wu, 1994). Generation mean analysis with four genetic models were used in this study.

Three-Parameter Genetic Model (Model 1)

The six means of generations P_1, P_2, F_1, F_2, B_1 ($P_1 \times F_1$) and B_2 ($P_2 \times F_1$) were used to estimate the model (Model 1, Mather and Jinks, 1982). The model contains three parameters: mean, additive, and dominance gene effects. To test the adequacy of the model, the residual error sum of squares was tested for goodness of fit using a chi-square statistic. The significance of each estimate was tested by t-test.

Six-Parameter Digenic Interaction Genetic Model (Model 2)

This model involves a three-parameter model and three digenic interactions of additive × additive [i], additive × dominant [j] and dominant × dominant [l] as described in Mather and Jinks (1982). The significance of the estimates was roughly evaluated with t-test by using the standard error of the estimates, but the model cannot be tested, because of lack of the degree of freedom.

Six-Parameter Synthetical Genetic Model (Model 3)

This model consists of the three-parameter genetic model (Model 1) and growing time [t]. It contains six parameters: [m], [d], [h], [t], [dt], and [ht], where parameter [t] is not a genetic parameter, [dt] and [ht] represent the interaction effects between growing time [t] and additive effect [d] and the dominance effect [h], respectively. The analytical model is shown in Formula (1).

The diagonal matrix **N** denotes the numbers of plants in six generations depending upon the basis on which the sample variances are computed. **S** is also a diagonal matrix containing sample variances. The matrix **C** consists of the expectations of genetic, growing time, and genetic-growing time interaction of the six generations at six growing times in terms of the six parameters, [m], [d], [h], [t], [dt], and [ht]. **Y** is a column vector of the generation means at six growing times. **M** is the vector of the genetic parameters to be estimated by the least squares method described by Rowe and Alexander (1980):

$$M = (C'NS^{-1}C)^{-1} C'NS^{-1} Y.$$

The model was tested by the following chi-square statistic.

$$\begin{pmatrix}
1 & 1 & 0 & 1 & 1 & 0 \\
1 & 0.5 & 0.5 & 1 & 0.5 & 0.5 \\
1 & 0 & 1 & 1 & 0 & 1 \\
1 & 0 & 0.5 & 1 & 0 & 0.5 \\
1 & -0.5 & 0.5 & 1 & -0.5 & 0.5 \\
1 & -1 & 0 & 1 & -1 & 0 \\
1 & 1 & 0 & 2 & 2 & 0 \\
1 & 0.5 & 0.5 & 2 & 1 & 1 \\
1 & 0 & 1 & 2 & 0 & 2 \\
1 & 0 & 0.5 & 2 & 0 & 1 \\
1 & -0.5 & 0.5 & 2 & -1 & 1 \\
1 & -1 & 0 & 2 & -2 & 0 \\
1 & 1 & 0 & 3 & 3 & 0 \\
1 & 0.5 & 0.5 & 3 & 1.5 & 1.5 \\
1 & 0 & 1 & 3 & 0 & 3 \\
1 & 0 & 0.5 & 3 & 0 & 1.5 \\
1 & -0.5 & 0.5 & 3 & -1.5 & 1.5 \\
1 & -1 & 0 & 3 & -3 & 0 \\
1 & 1 & 0 & 4 & 4 & 0 \\
1 & 0.5 & 0.5 & 4 & 2 & 2 \\
1 & 0 & 1 & 4 & 0 & 4 \\
1 & 0 & 0.5 & 4 & 0 & 2 \\
1 & -0.5 & 0.5 & 4 & -2 & 2 \\
1 & -1 & 0 & 4 & -4 & 0 \\
1 & 1 & 0 & 5 & 5 & 0 \\
1 & 0.5 & 0.5 & 5 & 2.5 & 2.5 \\
1 & 0 & 1 & 5 & 0 & 5 \\
1 & 0 & 0.5 & 5 & 0 & 2.5 \\
1 & -0.5 & 0.5 & 5 & -2.5 & 2.5 \\
1 & -1 & 0 & 5 & -5 & 0 \\
1 & 1 & 0 & 6 & 6 & 0 \\
1 & 0.5 & 0.5 & 6 & 3 & 3 \\
1 & 0 & 1 & 6 & 0 & 6 \\
1 & 0 & 0.5 & 6 & 0 & 3 \\
1 & -0.5 & 0.5 & 6 & -3 & 3 \\
1 & -1 & 0 & 6 & -6 & 0
\end{pmatrix}
\bullet
\begin{pmatrix} [m] \\ [d] \\ [h] \\ [t] \\ [dt] \\ [ht] \end{pmatrix}
=
\begin{pmatrix}
P_{11} \\ B_{11} \\ F_{11} \\ F_{21} \\ B_{21} \\ P_{21} \\ P_{12} \\ B_{12} \\ F_{12} \\ F_{22} \\ B_{22} \\ P_{22} \\ P_{13} \\ B_{13} \\ F_{13} \\ F_{23} \\ B_{23} \\ P_{23} \\ P_{14} \\ B_{14} \\ F_{14} \\ F_{24} \\ B_{24} \\ P_{24} \\ P_{15} \\ B_{15} \\ F_{15} \\ F_{25} \\ B_{25} \\ P_{25} \\ P_{16} \\ B_{16} \\ F_{16} \\ F_{26} \\ B_{26} \\ P_{26}
\end{pmatrix}
\quad \text{.....(1)}$$

$$\mathbf{C \times M = Y}$$

χ^2 = (Y-CM)'(NS^{-1})(Y-CM), df = k-p,

where k = the number of generation means, p = the number of parameters estimated.

The variances of the estimates **M** are the products of the diagonal elements of $\mathbf{(C'NS^{-1}C)^{-1}}$ and the $\chi^2/(k-p)$. These variances can be used to compute the Students t-test (df = k-p) or standard errors of the parameter estimates. The estimated values of the generation means **Y** may be obtained from using the parameters **M** and the genetic expectations **C,** i.e., **Y=CM**.

Twelve-Parameter Synthetical Genetic Model (Model 4)

This model is composed of a six-parameter genetic model and growing time (t). Overall there are twelve parameters: [m], [d], [h], [i], [j], [l], [t], [dt], [ht], [it], [jt] and [lt], where [it] is the interaction among additive × additive × growing time, [jt] is additive × dominant × growing time and [lt] is dominant × dominant × time growing. The analytical model is shown in Formula (2). The estimation and testing method is the same as that described in the previous model.

$$\begin{pmatrix}
1 & 1 & 0 & 1 & 0 & 0 & 1 & 1 & 0 & 1 & 0 & 0 \\
1 & 0.5 & 0.5 & 0.25 & 0.25 & 0.25 & 1 & 0.5 & 0.5 & 0.25 & 0.25 & 0.25 \\
1 & 0 & 1 & 0 & 0 & 1 & 1 & 0 & 1 & 0 & 0 & 1 \\
1 & 0 & 0.5 & 0 & 0 & 0.25 & 1 & 0 & 0.5 & 0 & 0 & 0.25 \\
1 & -0.5 & 0.5 & 0.25 & -0.25 & 0.25 & 1 & -0.5 & 0.5 & 0.25 & -0.25 & 0.25 \\
1 & -1 & 0 & 1 & 0 & 0 & 1 & -1 & 0 & 1 & 0 & 0 \\
1 & 1 & 0 & 1 & 0 & 0 & 2 & 2 & 0 & 2 & 0 & 0 \\
1 & 0.5 & 0.5 & 0.25 & 0.25 & 0.25 & 2 & 1 & 1 & 0.5 & 0.5 & 0.5 \\
1 & 0 & 1 & 0 & 0 & 1 & 2 & 0 & 2 & 0 & 0 & 2 \\
1 & 0 & 0.5 & 0 & 0 & 0.25 & 2 & 0 & 1 & 0 & 0 & 0.5 \\
1 & -0.5 & 0.5 & 0.25 & -0.25 & 0.25 & 2 & -1 & 1 & 0.5 & -0.5 & 0.5 \\
1 & -1 & 0 & 1 & 0 & 0 & 2 & -2 & 0 & 2 & 0 & 0 \\
1 & 1 & 0 & 1 & 0 & 0 & 3 & 3 & 0 & 3 & 0 & 0 \\
1 & 0.5 & 0.5 & 0.25 & 0.25 & 0.25 & 3 & 1.5 & 1.5 & 0.75 & 0.75 & 0.75 \\
1 & 0 & 1 & 0 & 0 & 1 & 3 & 0 & 3 & 0 & 0 & 3 \\
1 & 0 & 0.5 & 0 & 0 & 0.25 & 3 & 0 & 1.5 & 0 & 0 & 0.75 \\
1 & -0.5 & 0.5 & 0.25 & -0.25 & 0.25 & 3 & -1.5 & 1.5 & 0.75 & -0.75 & 0.75 \\
1 & -1 & 0 & 1 & 0 & 0 & 3 & -3 & 0 & 3 & 0 & 0 \\
1 & 1 & 0 & 1 & 0 & 0 & 4 & 4 & 0 & 4 & 0 & 0 \\
1 & 0.5 & 0.5 & 0.25 & 0.25 & 0.25 & 4 & 2 & 2 & 1 & 1 & 1 \\
1 & 0 & 1 & 0 & 0 & 1 & 4 & 0 & 4 & 0 & 0 & 4 \\
1 & 0 & 0.5 & 0 & 0 & 0.25 & 4 & 0 & 2 & 0 & 0 & 1 \\
1 & -0.5 & 0.5 & 0.25 & -0.25 & 0.25 & 4 & -2 & 2 & 1 & -1 & 1 \\
1 & -1 & 0 & 1 & 0 & 0 & 4 & -4 & 0 & 4 & 0 & 0 \\
1 & 1 & 0 & 1 & 0 & 0 & 5 & 5 & 0 & 5 & 0 & 0 \\
1 & 0.5 & 0.5 & 0.25 & 0.25 & 0.25 & 5 & 2.5 & 2.5 & 1.25 & 1.25 & 1.25 \\
1 & 0 & 1 & 0 & 0 & 1 & 5 & 0 & 5 & 0 & 0 & 5 \\
1 & 0 & 0.5 & 0 & 0 & 0.25 & 5 & 0 & 2.5 & 0 & 0 & 1.25 \\
1 & -0.5 & 0.5 & 0.25 & -0.25 & 0.25 & 5 & -2.5 & 2.5 & 1.25 & -1.25 & 1.25 \\
1 & -1 & 0 & 1 & 0 & 0 & 5 & -5 & 0 & 5 & 0 & 0 \\
1 & 1 & 0 & 1 & 0 & 0 & 6 & 6 & 0 & 6 & 0 & 0 \\
1 & 0.5 & 0.5 & 0.25 & 0.25 & 0.25 & 6 & 3 & 3 & 1.5 & 1.5 & 1.5 \\
1 & 0 & 1 & 0 & 0 & 1 & 6 & 0 & 6 & 0 & 0 & 6 \\
1 & 0 & 0.5 & 0 & 0 & 0.25 & 6 & 0 & 3 & 0 & 0 & 1.5 \\
1 & -0.5 & 0.5 & 0.25 & -0.25 & 0.25 & 6 & -3 & 3 & 1.5 & -1.5 & 1.5 \\
1 & -1 & 0 & 1 & 0 & 0 & 6 & -6 & 0 & 6 & 0 & 0
\end{pmatrix}
\bullet
\begin{pmatrix}
[m] \\ [d] \\ [h] \\ [i] \\ [j] \\ [l] \\ [t] \\ [dt] \\ [ht] \\ [it] \\ [jt] \\ [lt]
\end{pmatrix}
=
\begin{pmatrix}
P_{11} \\ B_{11} \\ F_{11} \\ F_{21} \\ B_{21} \\ P_{21} \\ P_{12} \\ B_{12} \\ F_{12} \\ F_{22} \\ B_{22} \\ P_{22} \\ P_{13} \\ B_{13} \\ F_{13} \\ F_{23} \\ B_{23} \\ P_{23} \\ P_{14} \\ B_{14} \\ F_{14} \\ F_{24} \\ B_{24} \\ P_{24} \\ P_{15} \\ B_{15} \\ F_{15} \\ F_{25} \\ B_{25} \\ P_{25} \\ P_{16} \\ B_{16} \\ F_{16} \\ F_{26} \\ B_{26} \\ P_{26}
\end{pmatrix}
\quad \text{.....(2)}$$

$$\mathbf{C \times M = Y}$$

Results and Discussion

Three-Parameter Genetic Model (Model 1)

The estimates of the three parameters and the test of goodness of fit of the model for leaf shape and size are given in Table 1. These results show that the additive-dominant model was adequate for leaf shape of top leaf in the sixth growing time, for leaf size of top leaf in the third and the middle and the lower leaf in the fourth growing time, but inadequate for the remaining cases. The estimates of m, [d] and [h] for the leaf size data sets will, therefore, be biased to an unknown extent by effects not attributable to the additive and dominance action of the genes.

The estimates of [d] are significantly different from zero in the case of whole growing time of middle leaf as well as top leaf at the sixth growing time of leaf shape, lower and middle leaf at the fourth growing time of leaf size. [h] is always negative and not significant in leaf shape and lower leaf size. For the case of leaf shape and lower leaf size, we may conclude that dominance may exist and that the genes producing small elongated leaf are in general dominant to the alleles which produce wide oval leaf. The dominance effect is not detected in the other cases. This three-parameter model fits only for top leaf shape, third growing time of top leaf and fourth growing time of middle and lower leaf of leaf size. Hence, it is difficult to illustrate the genetic mechanism of these two characters by this simple model.

Six-Parameter Digenic Interaction Genetic Model (Model 2)

This model is inadequate in both cases of leaf shape and size for three leaf positions and six growing times as shown in Table 2a and 2b. In this model, the parameters of m in leaf shape are significant for the three position leaves, but in the leaf size, parameters of [d] in the first and sixth growth stages of lower leaf are significant, and the others are not significant. The estimated values of [d] and [h] in top leaves, [d] in middle and [h] in lower leaves of leaf shape are negative. Digenic interaction of additive and additive [i] is negative in the top and lower leaves,

Table 1. Estimated values of three-parameter genetic model for leaf shape and leaf size.

		Time	[m]±SE	[d]±SE	[h]±SE	χ^2-value	p-value
Leaf shape	Top leaf	1	1.0805±0.0370	-0.0567±0.0320	-0.0197±0.0705	6.8071	0.10-0.05
		2	1.0869±0.0400	-0.0611±0.0343	-0.0199±0.0762	7.8081	0.05-0.02
		3	1.0881±0.0387	-0.0599±0.0332	-0.0213±0.0741	7.3850	0.10-0.05
		4	1.0865±0.0381	-0.0621±0.0327	-0.0121±0.0725	7.0738	0.10-0.05
		5	1.0904±0.0378	-0.0620±0.0323	-0.0213±0.0724	6.9446	0.10-0.05
		6	1.0928±0.0374	-0.0680±0.0322	-0.0227±0.0701	5.8724	0.20-0.10
	Middle leaf	1	1.1226±0.0284	-0.0630±0.0265	-0.0681±0.0560	18.4446	<0.001
		2	1.1257±0.0305	-0.0654±0.0282	-0.0639±0.0594	19.3003	<0.001
		3	1.1267±0.0320	-0.0654±0.0298	-0.0673±0.0622	21.1866	<0.001
		4	1.1276±0.0330	-0.0670±0.0304	-0.0663±0.0645	22.2391	<0.001
		5	1.1272±0.0321	-0.0659±0.0297	-0.0674±0.0627	20.8592	<0.001
	Lower leaf	1	1.0937±0.0280	0.0154±0.0232	-0.0080±0.0570	25.0092	<0.001
		2	1.0984±0.0269	0.0172±0.0220	-0.0125±0.0546	20.8814	<0.001
		3	1.0998±0.0276	0.0191±0.0225	-0.0145±0.0558	21.6263	<0.001
		4	1.0947±0.0348	0.0200±0.0267	-0.0059±0.0661	22.4957	<0.001
		5	1.0945±0.0355	0.0202±0.0271	-0.0047±0.0679	23.9656	<0.001
		6	1.0936±0.0361	0.0224±0.0276	-0.0041±0.0691	25.0021	<0.001
Leaf size	Top leaf	1	73.8854±17.7528	-23.8798±15.7579	-26.2071± 32.0247	24.6574	<0.001
		2	158.2997±34.3361	-16.7412±26.8408	-35.6525± 65.7449	15.7946	0.01-0.001
		3	217.0331±29.6276	-39.3119±25.1896	1.3875± 54.9964	11.2999	0.02-0.01
		4	248.1784±79.3901	-52.2165±68.6882	170.8888±137.5592	48.9588	<0.001
		5	347.7114±92.3329	-28.0647±83.6311	170.0970±172.6848	43.2287	<0.001
		6	351.8121±94.8635	-58.8778±92.0104	206.2271±161.0330	50.6828	<0.001
	Middle leaf	1	38.8794±16.1275	-21.9862±16.0080	10.9274± 28.7063	58.9309	<0.001
		2	135.8202±35.6713	-59.5279±35.1605	32.9538± 62.7103	36.3935	<0.001
		3	363.1434±36.2936	-83.8522±36.2913	-35.1670± 64.3437	14.4678	0.01-0.001
		4	485.1715±40.4655	-176.2054±32.1690	100.5146± 77.0624	5.3802	0.20-0.10
		5	472.9912±77.9618	-47.8750±77.2657	338.5448±124.6312	16.7989	<0.001
	Lower leaf	1	28.9793± 4.0228	-14.3861± 3.8643	-5.5204± 8.7164	27.6140	<0.001
		2	105.0848±12.6726	-35.3224±10.8443	10.4495± 26.2488	11.4225	0.01-0.001
		3	280.5666±34.6866	-103.8240±32.3476	-27.7509± 62.6576	18.3535	<0.001
		4	489.5882±38.4291	-148.8639±36.8831	-101.8200± 69.4883	11.1256	0.02-0.01
		5	562.5840±78.3891	-181.5055±68.3915	-123.0129±146.9426	31.0129	<0.001
		6	634.3486±54.8159	-209.5708±53.7526	-126.7299±100.3346	25.6080	<0.001

Table 2a. Estimated values of six-parameter genetic model and t-test for leaf shape.

	Time	[m] ± SE	[d] ± SE	[h] ± SE	[i] ± SE	[j] ± SE	[l] ± SE
Top leaf	1	1.2607±0.5732	-0.1247±0.1289	-0.5347±1.4514	-0.1202±0.5585	0.1923±0.4536	0.3483±0.9206
		2.1993*	-0.9671	-0.3684	-0.2152	0.4239	0.3783
	2	1.2918±0.5929	-0.1253±0.1279	-0.5870±1.4873	-0.1500±0.5789	0.1858±0.4569	0.3728±0.9382
		2.1788*	-0.9795	-0.3947	-0.2591	0.4077	0.3974
	3	1.2764±0.5942	-0.1284±0.1255	-0.5509±1.4882	-0.1294±0.5808	0.1953±0.4528	0.3547±0.9385
		2.1481*	-1.0231	-0.3701	-0.2228	0.4313	0.3780
	4	1.2781±0.6007	-0.1285±0.1290	-0.5596±1.5039	-0.1310±0.5867	0.1840±0.4594	0.3740±0.9469
		2.1278*	-0.9963	-0.3721	-0.2233	0.4006	0.3650
	5	1.2784±0.6020	-0.1277±0.1291	-0.5466±1.5055	-0.1316±0.5880	0.1854±0.4590	0.3484±0.9480
		2.1235*	-0.9892	-0.3631	-0.2238	0.4039	0.3675
	6	1.2753±0.6040	-0.1287±0.1344	-0.5391±1.5146	-0.1320±0.5888	0.1902±0.4674	0.3442±0.9547
		2.1116*	-0.9576	-0.3559	-0.2242	0.4069	0.3605
Middle leaf	1	1.0562±0.4430	-0.0673±0.0424	-0.0239±1.0748	0.0842±0.4409	-0.0319±0.2801	0.0971±0.6597
		2.3842*	-1.5880	-0.0222	-0.1910	-0.1139	0.1472
	2	1.0493±0.4427	-0.0693±0.0449	-0.0035±1.0772	0.0958±0.4405	-0.0344±0.2833	0.0898±0.6635
		2.3700*	-1.5426	-0.0032	0.2175	-0.1214	0.1353
	3	1.0429±0.4503	-0.0698±0.0448	0.0177±1.1005	0.1042±0.4480	-0.0402±0.2914	0.0770±0.6795
		2.3161*	-1.5570	0.0161	0.2326	-0.1379	0.1133
	4	1.0419±0.4432	-0.0717±0.0461	0.0187±1.0692	0.1070±0.4408	-0.0372±0.2770	0.0794±0.6554
		2.3508*	-1.5557	0.0175	0.2427	-0.1343	0.1211
	5	1.0452±0.4448	-0.0710±0.0458	0.0123±1.0818	0.1032±0.4424	-0.0349±0.2845	0.0805±0.6667
		2.3498*	-1.5500	0.0113	0.2333	-0.1227	0.1207
Lower leaf	1	1.2678±0.4174	0.0056±0.0343	-0.3336±0.9240	-0.1880±0.4160	0.0488±0.1846	0.1080±0.5310
		3.0371**	0.1634	-0.3610	-0.4519	0.2643	0.2034
	2	1.2457±0.4097	0.0057±0.0365	-0.2832±0.9128	-0.1622±0.4081	0.0541±0.1884	0.0809±0.5284
		3.0404**	0.1550	-0.3102	-0.3975	0.2871	0.1531
	3	1.2548±0.4239	0.0072±0.0371	-0.2973±0.9392	-0.1710±0.4223	0.0515±0.1897	0.0859±0.5400
		2.9601**	0.1927	-0.3165	-0.4050	0.2714	0.1591
	4	1.2442±0.4243	0.0175±0.0500	-0.2655±0.9417	-0.1720±0.4213	0.0299±0.2001	0.0651±0.5420
		2.9323**	0.3488	-0.2819	-0.4082	0.1494	0.1201
	5	1.2512±0.4253	0.0168±0.0495	-0.2797±0.9433	-0.1788±0.4224	0.0312±0.1995	0.0730±0.5426
		3.9320**	0.3394	-0.2965	-0.4233	0.1564	0.1345
	6	1.2576±2.4276	0.0165±0.0488	-0.2975±0.9480	-0.1848±0.4248	0.0395±0.1995	0.0839±0.5451
		2.9481**	0.3370	-0.3138	-0.4350	0.1980	0.1539

* and **, Significant at 5% and 1% level, respectively for t-test, but the model can not be tested.

Table 2b. Estimated values of six-parameter genetic model and t-test for leaf size.

	Time	[m] ± SE	[d] ± SE	[h] ± SE	[i] ± SE	[j] ± SE	[l] ± SE
Top leaf	1	71.7020±186.5609	-36.3770±27.5873	-91.7260±428.9410	21.8440±184.5099	16.4100±105.2157	106.6560±253.9791
		0.3843	-1.3186	-0.2138	0.1184	0.1560	0.4199
	2	70.5050±306.0199	-26.5660±58.5090	109.0050±752.9091	118.2640±300.3746	-6.7920±218.7079	-7.8340±473.4877
		0.2304	-0.4541	0.1448	0.3937	-0.0311	-0.0165
	3	102.4090±428.3975	-44.1600±57.5496	205.2340±993.2488	140.0440±424.5143	-4.4960±244.3216	-57.0360±589.4362
		0.2391	-0.7673	0.2066	0.3299	-0.0184	-0.0968
	4	206.5400±496.2650	-144.4770±94.7350	32.2480±1180.2511	183.5320±487.1388	157.5380±328.0597	270.1120±711.2686
		0.4162	-1.5251	0.0273	0.3768	0.4802	0.3798
	5	384.8585±611.9567	-124.8775±96.5970	-205.8465±1513.4248	104.1620±604.2847	274.3490±429.8000	464.4310±938.0610
		0.6289	-1.2928	-0.1360	0.1724	0.6383	0.4951
	6	384.8585±715.6291	-124.8775±90.7490	-205.8465±1706.8122	104.1620±709.8518	274.3490±443.4438	464.4310±1023.7381
		0.5379	-1.3761	-0.1206	0.1467	0.6187	0.4537
Middle leaf	1	6.1365±167.9367	-12.5065±12.8175	173.2135±394.0122	20.6080±167.4469	-6.0750±94.4661	-157.8850±233.6983
		0.0365	-0.9757	0.4396	0.1231	-0.0643	-0.6756
	2	0.8975±388.2843	-34.2625±38.0520	523.1965±937.1256	104.1080±386.4153	-62.5310±242.7282	-420.7270±568.8623
		0.0023	-0.9004	0.5583	0.2694	-0.2576	-0.7396
	3	222.0425±615.6557	-70.3175±56.8309	482.3445±1539.5571	102.8740±613.0271	-111.6230±423.8182	-424.0590±952.1610
		0.3607	-1.2373	0.3133	0.1678	-0.2634	-0.4454
	4	434.9670±792.0094	-175.4330±105.9102	82.9700±1869.6356	93.1420±784.8961	-13.1120±476.3538	142.6760±1134.6862
		0.5492	-1.6564	0.0444	0.1187	-0.0275	0.1257
	5	554.8255±958.9774	92.1655±147.5321	56.3135±2308.3992	-21.1440±947.5610	-466.2910±627.5205	227.2030±1391.4105
		0.5786	0.6247	0.0244	-0.0223	-0.7431	0.1633
Lower leaf	1	71.8280±138.9554	-12.5550±3.8038	-72.5320±297.1712	-43.7380±138.9034	-24.0800±47.2835	20.5680±162.3095
		0.5169	-3.3006**	-0.2441	-0.3149	-0.5093	0.1267
	2	133.4025±235.9724	-27.9155±20.6328	-6.2815±537.2593	-33.9700±235.0687	-41.5230±118.6263	-41.2470±319.1077
		0.5653	-1.3530	-0.0117	-0.1445	-0.3500	-0.1293
	3	140.8410±454.5566	-61.8870±48.2896	383.8200±1096.5607	129.5760±451.9843	-243.6820±285.5989	-275.4840±665.3936
		0.3098	-1.2816	0.3500	0.2867	-0.8532	-0.4140
	4	262.4050±579.0507	-114.5520±70.1148	548.5230±1420.8154	197.9060±574.7901	-180.7220±386.0578	-440.9420±873.1549
		0.4532	-1.6338	0.3861	0.3443	-0.4681	-0.5050
	5	207.2405±667.2376	-114.4625±82.3434	740.8025±1597.7313	375.0640±662.1371	-369.1230±415.4046	-465.1870±972.1919
		0.3106	-1.3901	0.4637	0.5664	-0.8886	-0.4785
	6	439.2275±691.6718	-168.4165±63.9537	250.1595±1661.5930	237.1820±688.7088	-266.8290±424.8234	-126.0130±1003.9604
		0.6350	-2.6334	0.1506	0.3444	-0.6281	-0.1255

**, Significant at 1% level for t-test, but the model can not be tested.

additive and dominance interaction [j] is negative in the middle leaves of leaf shape. In the leaf size, [d] is negative in three leaf positions, and digenic interaction of [j] also shows negative in middle leaves. The dominance effect is positive; hence, large leaf size is dominant over small leaf size in the three kinds of leaves. In the leaf shape, the dominance effect [h] is negative in the top and lower leaves, which shows that the small shape index (i.e., elongated leaf) is dominant over the large shape index, (i.e., oval leaf). In the middle leaves, however, [h] is positive and oval leaf is dominant over elongated leaf; therefore, the inheritance mechanism is different for differently positioned leaves of tobacco in this study.

Six-Parameter Synthetical Genetic Model (Model 3)

The fitting result is shown in Table 3. In this model, only a case of top leaves appears adequate for shape. In leaf size, none of the cases are adequate for this model. In leaf shape, the m value is significant in three types of leaves, and the [d] effect is significant in top and middle leaves. The dominance effect [h] is negative, which indicates that elongated leaf is dominant over oval leaf in the three types of leaves. The interaction effect of [dt] and [ht] has a negative value but is not significant in the top and middle leaves. In leaf size, the m value of middle and lower leaves, [h] and [ht] of top leaf, [dt] and [ht] of middle leaves, as well as [d] and [dt] of lower leaves are significant. The [h] value is negative in top and middle leaves, and hence small leaf size is dominant over large size. Conversely, large leaf size and elongated leaves are dominant in lower leaves. These two characters seem not to appear in the same leaf because an elongated tobacco leaf is always small. Therefore, this genetic model seems inadequate to illustrate the mechanism of inheritance of these two characters.

Table 3. Estimated values of synthetic six-genetic model of leaf shape and leaf size.

Parameter	Top leaf	Middle leaf	Lower leaf
Leaf shape			
[m] ± SE	1.0803±0.0275	1.1225±0.0254	1.0971±0.0205
[d] ± SE	-0.0555±0.0237	-0.0630±0.0236	0.0146±0.0167
[h] ± SE	-0.0185±0.0523	-0.0662±0.0498	-0.0128±0.0413
[t] ± SE	0.0021±0.0072	0.0011±0.0078	-0.0004±0.0057
[dt] ± SE	-0.0017±0.0062	-0.0008±0.0072	0.0012±0.0045
[ht] ± SE	-0.0003±0.0136	-0.0001±0.0152	0.0012±0.0113
χ^2-value	42.1804	102.3264	139.4001
p-value	0.01-0.05	<0.001	<0.001
Leaf size			
[m] ± SE	8.3140±23.1547	-84.5472±22.4436	-93.3931±10.3052
[d] ± SE	-19.5849±20.7022	16.2754±21.9521	23.3019± 9.7522
[h] ± SE	-90.5329±41.7676	-49.3638±39.2268	7.2340±20.1784
[t] ± SE	66.2812± 9.6627	122.6094±15.0621	120.6679± 8.4322
[dt] ± SE	-3.5561± 8.7905	-39.3015±14.5195	-36.2757± 7.8953
[ht] ± SE	53.4867±17.2039	53.9429±26.0687	-12.7133±15.7787
χ^2-value	248.8221	273.4894	346.4372
p-value	<0.001	<0.001	<0.001

Twelve-Parameter Synthetical Genetic Model (Model 4)

The analysis results are displayed in Table 4. This model fits very well for leaf shape of three types of leaves, but is inadequate for leaf size. In leaf shape, the estimated values of m are all significant for the three types of leaves, [d] and [h] of top leaf, [d] and [it] of middle leaf, and [h] [dt] and [ht] of lower leaf are also significant. The digenic interaction effect of [i], [j] and [l] are all significant for the three types of leaves, but are insignificant in Model 2. The interaction of additive x additive x growth time is significant at middle leaves, showing that the digenic interaction effect of additive and additive changes with the growth. On the other hand, [dt] and [ht] are also significant at lower leaves. The [h] value is negative in this character for three types of leaves, so elongated leaf is dominant over oval leaf. [ht] is significant, indicating elongated leaf shape is influenced by growth.

In leaf size, only the parameter of [dt] is significant at lower and middle leaves, indicating that the additive effect causes changes in growth. The [h] is negative in top and lower leaves; hence, small size is dominant over large

Table 4. Estimated values of synthetic twelve-genetic model for leaf shape and size.

Parameter	Top leaf	Middle leaf	Lower leaf
Leaf shape			
[m] ± SE	1.2716±0.0123	1.0559±0.0064	1.2575±0.0090
[d] ± SE	-0.1246±0.0061	-0.0669±0.0016	0.0018±0.0022
[h] ± SE	-0.5590±0.0339	-0.0240±0.0169	-0.3137±0.0217
[i] ± SE	-0.1303±0.0106	0.0840±0.0062	-0.1724±0.0087
[j] ± SE	0.1919±0.0147	-0.0330±0.0055	0.0561±0.0064
[l] ± SE	0.3631±0.0241	0.0978±0.0118	0.0985±0.0148
[t] ± SE	0.0013±0.0032	-0.0029±0.0019	-0.0009±0.0023
[dt] ± SE	-0.0007±0.0016	-0.0010±0.0005	0.0025±0.0006
[ht] ± SE	0.0022±0.0088	0.0094±0.0051	0.0533±0.0057
[it] ± SE	-0.0004±0.0028	0.0050±0.0019	-0.0010±0.0022
[jt] ± SE	-0.0010±0.0038	-0.0009±0.0017	-0.0033±0.0018
[lt] ± SE	-0.0020±0.0063	-0.0043±0.0035	-0.0040±0.0039
χ^2-value	0.6189	0.2232	0.9925
p-value	>0.99	>0.99	>0.99
Leaf size			
[m] ± SE	-14.4932± 56.3106	-107.5707±118.4952	3.3525± 76.2156
[d] ± SE	-20.6174± 19.9297	28.2104± 26.9545	12.7610± 11.7093
[h] ± SE	-42.5782±144.8293	102.5498±299.6907	-199.0309±184.7687
[i] ± SE	13.6196± 52.6659	11.7969±115.3888	-98.7448± 75.3108
[j] ± SE	-18.9932± 52.5024	-2.3848± 93.4439	55.3644± 50.1572
[l] ± SE	-5.4273± 98.6671	-161.7505±193.0163	102.3642±116.8349
[t] ± SE	62.0201± 23.0148	102.6689± 70.1423	67.3159± 40.1370
[dt] ± SE	-12.7594± 7.9330	-40.4479± 18.2563	-24.5248± 9.9647
[ht] ± SE	14.9241± 59.7379	97.0464±180.1118	114.6919±104.5105
[it] ± SE	29.3374± 21.6044	17.7599± 67.7249	54.6253± 38.8804
[jt] ± SE	25.3487± 21.6170	-8.2428± 59.0164	-66.1019± 34.0935
[lt] ± SE	57.6640± 39.9351	-21.7153±117.2592	-70.3757± 69.4899
χ^2-value	70.4222	184.9394	269.1164
p-value	<0.001	<0.001	<0.001

size, but in middle leaves large size is dominant. It is impossible to accurately change gene direction in the same character during plant growth; therefore, this model can not illustrate the inheritance of leaf size.

Genetic Models and the Inheritance of Leaf Size

Among the four models, a best fitted model for these two leaf characters is selected. The summarized result is shown in Table 5. The three-parameter simple genetic model is adequate for top leaf shape, the third growth stage of top, and the fourth growth stage of middle and lower leaf size. The six-parameter digenic interaction genetic model is inadequate for these two leaf characters. The six-parameter synthetical genetic model is adequate only for the top leaf shape. The twelve-parameter synthetical genetic model is adequate for leaf shape for three position leaves, but inadequate for leaf size.

Therefore, we may conclude that the twelve-parameter model is suitable to illustrate the inheritance of leaf shape, but we can not find an adequate model to depict the inheritance mechanism of leaf size. Park et al. (1994) studied the inheritance of leaf size of the first trifoliolate leaf in common bean and concluded that the additive, dominance, and epistatic gene interactions control the mecha-

Table 5. A summary of testing results of four model.

		Top leaf	Middle leaf	Lower leaf
Leaf shape				
Three-parameter genetic model	Model Parameters [m],[d],[h]	Adequate [m],[d_6] sig. [d],[h] neg.	Inadequate [m],[d] sig. [d],[h] neg.	Inadequate [m] sig. [h] neg.
Six-parameter digenic interaction genetic model	Model Parameters [m],[d],[h],[i],[j],[l]	Inadequate [m] sig. [d],[h],[i] neg.	Inadequate [m] sig. [d],[j] neg.	Inadequate [m] sig. [h],[i] neg.
Six-parameter synthetical genetic model	Model Parameters [m],[d],[h],[t],[dt],[ht]	Adequate [m],[d] sig. [d],[h],[dt],[ht] neg.	Inadequate [m],[d] sig. [d],[h],[dt],[ht] neg.	Inadequate [m] sig. [h] neg.
Twelve-parameter synthetical genetic model	Model Parameters [m],[d],[h],[I],[j],[l],[t], [dt],[ht],[it],[jt],[lt]	Adequate [m],[d],[h],[i],[j],[l] sig. [d],[h],[i],[dt],[it],[jt], [lt] neg.	Adequate [m],[d],[i],[j],[l],[it] sig. [d],[h],[j],[dt],[jt],[lt] neg.	Adequate [m],[h],[i],[j],[l],[dt],[ht] sig. [h],[i],[it],[jt],[lt] neg.
Leaf size				
Three-parameter genetic model	Model Parameters [m],[d],[h]	t=3 adequate [m] sig. [d],[h] neg.	t=4 adequate [m],[d_3],[d_4],[h_5] sig. [d] neg.	t=4 adequate [m],[d] sig. [d],[h] neg.
Six-parameter digenic interaction genetic model	Model Parameters [m],[d],[h],[i],[j],[l]	Inadequate All no sig. [d] neg.	Inadequate All no sig. [d],[j] neg.	Inadequate [d_1],[d_6] sig. [d] neg.
Six-parameter synthetical genetic model	Model Parameters [m],[d],[h],[t],[dt],[ht]	Inadequate [h],[ht] sig. [dt],[ht] neg.	Inadequate [m],[dt],[ht] sig. [h],[dt] neg.	Inadequate [m],[d],[dt] sig. [h],[dt] neg.
Twelve-parameter synthetical genetic model	Model Parameters [m],[d],[h],[i],[j],[l],[t], [dt],[ht],[it],[jt],[lt]	Inadequate All no sig. [d],[h],[j],[l],[dt] neg.	Inadequate [dt] sig. [j],[l],[dt],[jt],[lt] neg.	Inadequate [dt] sig. [h],[i],[dt],[it],[lt] neg.

Sig.=Significant at 5 or 1% level by t-test; Neg.= Negative estimated value.

Table 6. Dominant character from analysis results.

	Top leaf	Middle leaf	Lower leaf
Leaf shape (oval leaf vs elongated leaf)			
Three-parameter genetic model	Elongated leaf	Elongated leaf	Elongated leaf
Six-parameter digenic interaction genetic model	Elongated leaf	Oval leaf	Elongated leaf
Six-parameter synthetical genetic model	Elongated leaf	Elongated leaf	Elongated leaf
Twelve-paramter synthetical genetic model	Elongated leaf	Elongated leaf	Elongated leaf
Leaf size (large size vs small size)			
Three-parameter genetic model	Small size	Large size	Small size
Six-parameter digenic interaction genetic model	Large size	Large size	Large size
Six-parameter synthetical genetical model	Small size	Small size	Large size
Twelve-parameter synthetical genetic model	Small size	Large size	Small size

nism of inheritance of leaf area, but the joint-scaling tests based on either the three-parameter (additive-dominance) model or the six-parameter digenic interaction (additive-dominance intearction) model did not fit, indicating that neither model was adequate for leaf area. The same results are also obtained by our study. Shopova and Jordanov (1990) also studied the inheritance of ear leaf area in maize. Their result showed that the size of maize ear leaf depends on both genotypes and environments during the growth period. Dominance gene effect [d] is the major factor controlling ear leaf formation of maize. Gene interaction of [i] and [l] also has a share in the control of the character. In tobacco leaf area, the [h] and [l] may contribute more for variation of leaf size than [d] and [i].

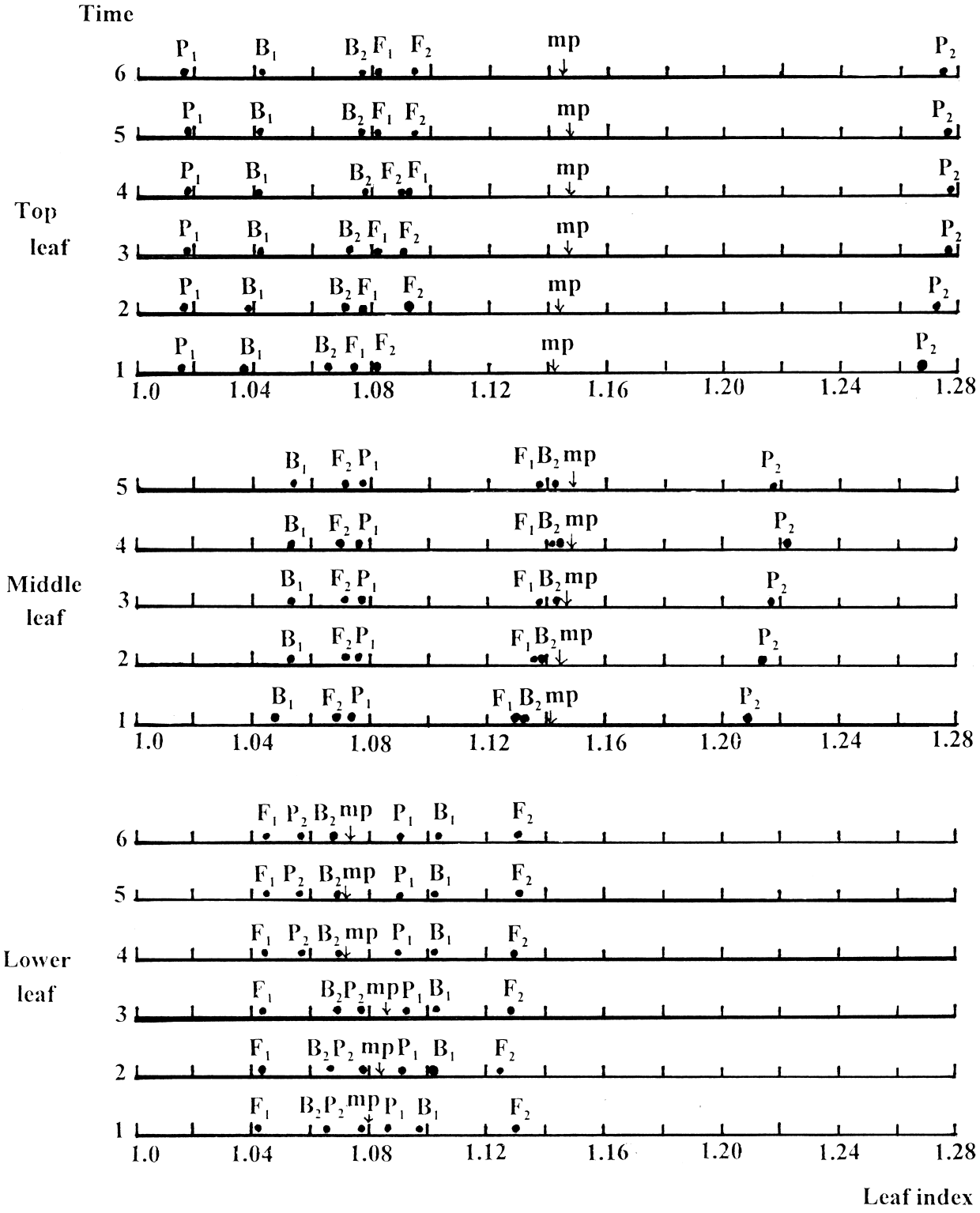

Figure 1. The diagram of leaf index of leaf shape for various generations in different growth times of three leaf positions.

The dominant character of leaf size varies with different genetic models and leaf positions. In Model 1, the dominant characters of top and lower leaves are small size, but for the middle leaves it is large size. In Model 2, large size is dominant for three types of leaves. In Model 3, small size is dominant for the top and middle leaves, but recessive for lower leaves. In Model 4, small size is dominant in the top and lower leaves, but recessive in the middle leaves (Table 6). Therefore, we can not conclude and illustrate the inheritance of leaf size for tobacco leaves. Leaf size was determined by genetics and environment (Gurevitch, 1992); hence it may be suitable to illustrate the genetic mechanism for leaf size in a fixed position of single leaf, or increase the number of planted locations to increase the generational mean. This would allow us to estimate the effect of genetic-environmental interaction and understand the inheritance of leaf size.

Genetic Models and Inheritance of Leaf Shape

For leaf shape, the twelve-parameter model is capable of illustrating the inheritance of tobacco leaf shape as shown in Table 5. The estimated values of various parameters are shown in Table 4. This model indicates that additive, dominant, and epistatic genes control the leaf shape, and these gene effects may change and cause physiological processes to change during growth. The additive gene effect [d] has negative value for the top and middle leaves, but positive value for the lower leaves. The dominant gene effect [h] is negative, indicating that the elongated leaf is dominant (Table 6). The digenic interaction of additive × additive [i] is negative for the top and lower leaves, but the additive effects [d] of these two leaves have negative and positive values, respectively. For the middle leaves, the value [d] is negative, and the value [i] is positive. This shows that two negative additive effects interact. The dominant × dominant effect [l] is positive, but all dominant effect of [h] is negative. The additive × dominant interaction effect of [j] has either positive or negative value for the top, lower, and middle leaves. This is not a clear result for illustrating a genetic mechanism.

The interactions between various gene effects and growth time is not significant except for the [it] of the middle leaves, and [dt] and [ht] effects of the lower leaves. It means that the additive × additive effect [i] of middle leaves, additive effect [d], and dominant effect [h] of lower leaves will change during growth.

The diagram of leaf shape index for six generations in different growth times of three leaves is shown in Figure 1. The index values are different in the three types of leaves. The range of shape index has the largest value in the top leaves and the smallest values in the lower leaves. This shows that the top leaves have more shapes than the lower leaves, because as the plant approaches maturity, the shape of the top leaves will be more affected by the environment. For the top leaves, P_2's index is the largest and P_1's index is the smallest. F_1 and F_2 , B_1 and B_2 are located in the left side of mid-parent value (MP). This means that the small index (elongated leaf) is dominant or partial dominant. This result is the same as that shown in Table 6. For the middle leaves, P_2 also has the largest index and B_1 has the smallest index. This indicates that the variety of leaf shapes in the middle leaves is less than that at the top. The index of the lower leaves has the smallest value among these three types of leaves. Therefore, there is less leaf shape variety than for the other two types. F_2's leaves have an oval type, and F_1 has an elongated type.

Adamson (1983) studied the inheritance of leaf type of *Hibiscus sabdariffa* and concluded that the narrowly lobed type is dominant over the non-lobed type; monogenic effect controls the inheritance; and there is an allelic series govering the leaf shape, but existence of two loci cannot be ruled out. Branch (1987) proved that a single recessive gene controls the curly-leaf characteristic of peanut leaf shape. Geltink (1983) found that a mono or digenically dominant inheritance mechanism may regulate the leaf shape of turnip and an incomplete monogenically dominant genetic system has control of rape leaf shape. Our results indicate that tobacco leaf shape is controlled by the twelve-parameter genetic model, that digenic interaction may change during growth, and that narrow leaf shape may be dominant over oval leaf type.

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