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Genetic analysis of *Verticillium* wilt tolerance in cotton using pedigree data from three crosses*

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Summary. Three crosses and descendant generations were used in a field study of the inheritance of tolerance to *Verticillium* wilt, caused by *Verticillium dahliae* Kleb., in upland cotton (*Gossypium hirsutum* L.). The tolerant cultivar 'Acala SJC-1' was crossed to more susceptible parents, breeding line S5971 and cultivars 'Acala 4-42' and 'Deltapine 70'. Seven generations were evaluated for each cross: the two parents (P_1 and P_2), F_1, F_2, F_3, and reciprocal backcrosses (B_1 and B_2). The genetic control of tolerance in these crosses appears to involve more than one gene, based on an unsatisfactory fit to expected phenotypic distributions for the generations under a single-locus model. An analysis of generation means indicated that pooled additive and pooled dominance effects over loci were adequate to explain the variation among generations for crosses of SJC-1 × S5971 and SJC-1 × DPL 70. Tolerance in these crosses appeared to be controlled by recessive factors. For the SJC-1 × 4-42 cross, an adequate fit to a digenic epistatic model was not possible, and none of the genetic parameters except the F_2 mean were significant. Heritabilities for tolerance to *Verticillium* wilt, determined from regressions of F_3 progeny on F_2 parents for the crosses of SJC-1 × S5971 and SJC-1 × DPL 70, ranged from 0.12 to 0.28. Therefore, individual plant selection for improved tolerance is expected to be inefficient.

Key words: *Gossypium hirsutum L. – Verticillium dahliae Kleb.* – Generation means analysis – Minimum chi-square – Genetic segregation

Introduction

It is generally accepted that *Verticillium* wilt, caused by *Verticillium dahliae,* Kleb., is one of the most important diseases of cotton (*Gossypium hirsutum* L.). The disease is known to occur on all continents and in most cotton growing areas. In the San Joaquin Valley of California, where the present study was conducted, *Verticillium* wilt is a chronic problem which can result in fiber losses exceeding 100,000 bales annually (Gazaway 1983).

Severity of *Verticillium* wilt, as observed by the expression of disease symptoms, is influenced by a number of environmental factors including: inoculum density, the strain or pathotype of the fungus, soil moisture, planting density, and high air and soil temperatures (Pullman and DeVay 1982a, b). A single genotype can give rise to a range of phenotypic expressions for wilt tolerance depending on the influence of these factors. This variation complicates a genetic interpretation of the trait, requiring the use of appropriate statistical methods for studies of inheritance. One such method was proposed by Elston (1981) and is used in this paper to test for single-locus segregation of disease tolerance.

Various accounts for the inheritance of *Verticillium* wilt tolerance in cotton have been reported. Wilhelm et al. (1969, 1970) concluded from studies of interspecific crosses between tolerant cultivars of *G. barbadense* and susceptible cultivars of *G. hirsutum* that tolerance in such crosses was determined by a single dominant or partially dominant factor. Similar results were reported by Bell and Presley (1969).

In intraspecific *G. hirsutum* crosses, tolerance has been more difficult to characterize. Barrow (1973), using a specific temperature regime and SS-4, a non-

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** Present address: Soil and Crop Sciences Department, Texas A & M University, College Station, TX 77843, USA defoliating isolate of *V. dahliae*, obtained segregation ratios suggesting a single dominant factor in F_1, F_2, and backcross generations of tolerant 'Acala 9519' × susceptible 'Acala 227'. However, these results were not confirmed in field tests where a defoliating strain predominated. Barnes and Staten (1961) found that tolerant × susceptible cotton crosses generally produced susceptible F_1 plants. Roberts and Staten (1972) reported that tolerance to *Verticillium* wilt was recessive in the materials they studied. Stith (1969) and Verhalen et al. (1971) reported that tolerance in *G. hirsutum* is quantitatively rather than qualitatively inherited. It seems fairly well established that in interspecific crosses a dominant gene controls *Verticillium* wilt tolerance under field and laboratory conditions (Bell and Presley 1969; Wilhelm et al. 1969, 1970). However, there may be different sources of tolerance in the *G. hirsutum* germplasm, and the type of inheritance observed may depend on the materials used for evaluation.

The purpose of this investigation is first to test for single-locus segregation of *Verticillium* wilt tolerance in generations derived from three *G. hirsutum* crosses. Secondly, genetic effects for tolerance are estimated by an analysis of generation means, assuming a quantitative inheritance. Finally, parent-progeny regression is used to estimate narrow-sense and realized heritabilities of *Verticillium* wilt tolerance in two of the three crosses.

Materials and methods

The study to test a one-locus segregation hypothesis and determine gene effects, consisted of three experiments involving generations derived from crosses of 'Acala SJC-1 × S5971, Acala SJC-1 × 'Acala 4-42', and Acala SJC-1 × 'Deltapine 70'. Each experiment included the parents (P_1 and P_2), F_1, F_2, F_3, and reciprocal backcrosses (B_1 and B_2). In each experiment P_1 was SJC-1, which was used as a wilt-tolerant cultivar in the San Joaquin Valley following its release in 1983. SJC-1 was derived from a cross of (C6TE × B3080) × (NM7403 × 4-42-77). P_2 was a more susceptible parent, either S5971, 4-42, or DPL 70. Breeding line S5971 was developed at the USDA Cotton Research Station at Shafter, California, and has some Tanguis (*G. barbadense*) background: [12302-4 × (Tanguis × 4-42)] × (C6-5 × Del Cerro 503). Acala 4-42 was used to control *Verticillium* wilt in the San Joaquin Valley for about 15 years, and was originally derived from Acala 1517-4 × Missdel (Turner 1974). The 1966 "model" (year of valley-wide use) was used in this study. DPL 70 was selected from Stoneville 70 × 6621-723-81.

The materials from these crosses were evaluated on the Wilcox farm near Plainview, California. This location is also used by the California Planting Cotton Seed Distributors for evaluating *Verticillium* wilt tolerance in lines being developed for release in the San Joaquin Valley. Microsclerotial counts of *V. dahliae* determined from a bulk of eight samples, were 20–30/gm of air-dry soil, using the method of Huisman and Ashworth (1974). The soil was an Exeter (fine-loamy, mixed, thermic Typic Durixeralfs).

The seed were machine planted on 16 April, 1985 in a completely randomized design with three replications for each cross combination. Each plot consisted of 25–35 plants in a row 7.6 m long, with an inter-row spacing of 1 m. Cultural practices considered normal for the area were followed, including two mid-season irrigations.

Environmental conditions were favorable for *Verticillium* wilt; symptom expression was severe and uniform within experiments. Based on disease reaction of the common entry SJC-1, the experiment including SJC-1 × S5971 appeared to have a somewhat lower severity of *Verticillium* wilt. On September 3, 20 plants/plot of the segregating generations and 10 plants/plot of the parental and F_1 generations were rated for *Verticillium* wilt susceptibility on a scale of 0–5: 0 = no visible leaf symptoms; 1 = mild to moderate leaf symptoms; 2 = severe leaf symptoms, little defoliation; 3 = 50–75% defoliation; 4 = up to 90% defoliation, some terminal dieback, plants often stunted; 5 = complete defoliation, stems dying back or dead to ground level. To reduce border effects, two plants on each end of the plot were not included in the evaluations.

A modified minimum χ^2 test following Elston (1981) was used to determine whether single-locus segregation could account for observed distributions of tolerance to *Verticillium* wilt among the various generations of the crosses. Briefly, the phenotypic values were divided into k intervals (here k = 2, 3 . . . 6). Assuming a single-locus model, the number of individuals (x_{ij}) in the ith generation and jth interval follow a multinomial distribution with expected cell probabilities shown in Table 1. Here α_{0j}, α_{1j}, and α_{2j} are expected frequencies of P_1, F_1, and P_2 generations, respectively, in the jth interval. With appropriate estimates of the probabilities (p_{ij}), a χ^2 statistic to test the goodness of fit for the proposed model may be calculated as follows:

$$\sum_{i=1}^{7}\sum_{j=1}^{k}\left[\frac{(X_{ij}-n_i\,p_{ij})^2}{n_i\,p_{ij}}\right]$$

where i, j, k, x_{ij}, and p_{ij} are as alluded to above, and n_i is the number of individuals in the ith generation. Estimates of p_{ij} were obtained by minimizing a χ^2 modified by substitution of observed numbers for expected numbers in the denominator. Thus, using the values for p_{ij} in Table 1, we minimized:

$$\sum_{j=1}^{k}\left\{\frac{(x_{1j}-n_1\,\alpha_{0j})^2}{x_{1j}}+\frac{[x_{2j}-n_2(\alpha_{0j}+\alpha_{1j})/2]^2}{x_{2j}}+\frac{(x_{3j}-n_3\,\alpha_{1j})^2}{x_{3j}}\right.$$
$$+\frac{[x_{4j}-n_4(\alpha_{0j}+2\,\alpha_{1j}+\alpha_{2j})/4]^2}{x_{4j}}+\frac{[x_{5j}-n_5(\alpha_{1j}+\alpha_{2j})/2]^2}{x_{5j}}$$
$$\left.+\frac{(x_{6j}-n_6\,\alpha_{2j})^2}{x_{6j}}+\frac{[x_{7j}-n_7(3\,\alpha_{0j}+2\,\alpha_{1j}+3\,\alpha_{2j})/8]^2}{x_{7j}}\right\}.$$

Minimization of the function was accomplished by equating to zero the partial derivatives with respect to α_{ij} (i = 0, 1, 2; j = 1, 2 . . . k − 1). The result was a set of 3(k − 1) equations linear in α_{ij}, the solution of which gave the desired estimates. The α's for the last interval were calculated by subtraction from 1. These estimates were then used in calculating p_{ij} in the above equation to obtain a χ^2 for testing the single-locus hypothesis (Elston 1981).

A generation means analysis (Hayman 1958) was used to estimate the contribution of several genetic effects to the variation among generation means. Gamble's (1962) notation for the genetic parameters was used, i.e., m equals the F_2 mean; a and d are pooled additive and pooled dominance effects over all loci; aa, ad, and dd are the pooled digenic additive × additive, the additive × dominance, and the dominance × dominance interaction effects, respectively. Each of the three crosses was analyzed separately. The inverse of the variance of the generation means was used as a weighting factor in least squares procedures as outlined by Rowe and Alexander (1980). Genetic parameters were used in various combinations to obtain a nonsignificant ($P < 0.05$) fit, as determined by a χ^2 test which included the fewest parameters.

In two additional experiments, parent-progeny regression was used to estimate the heritabilities for tolerance to Verticillium wilt in crosses SJC-1 × S5971 and SJC-1 × DPL 70. The mean of 50 F_3 families (20 plants/family), over two replications, were regressed on their F_2 parents which had been grown and evaluated for wilt tolerance the previous year (1984). Heritabilities in the narrow sense were estimated from regression coefficients, b, of actual data and data coded in terms of standard deviation units (Frey and Horner 1957) as $h^2 = (2/3)$ b, consistent with parent-offspring studies (Smith and Kinman 1965). Realized heritabilities were also calculated as the proportion, R/S, of the selection differential (S) made in the parental generation that was retained in the progeny of the selected sample in the subsequent generation (the response, R) (Falconer 1981). The selection intensity was 10% of the F_2 population. Significance was assigned to the realized heritability values using a *t*-test of the proportion of the selection differential retained, $R/s\bar{d} = t$ (Steel and Torrie 1980).

Results and discussion

Test of a single-locus model

Frequency distributions for *Verticillium* wilt tolerance of parental and F_1 generations in the three crosses indicate the range of phenotypic expression associated with each genotype (Fig. 1 A, B, C). Classification of the individuals is difficult as a result of environmental variation and experimental error. The distributions of wilt tolerance in the segregating generations have little or no bimodality (Devey 1986), and it is not clear whether they are consistent with segregation at a single locus.

In the crosses of SJC-1 × S5971 and SJC-1 × DPL 70 (Fig. 1 A, C), the factor(s) appears to be recessive (susceptibility is dominant), since the distribution of the F_1 closely approximates that of the P_2, the more susceptible parent. Dominance is not evident in the SJC-1 × 4-42 cross (Fig. 1 B).

Elston (1981) has presented a method for genetic analysis of a trait whose manifestation is influenced to a large extent by environment. Following this method, total χ^2 statistics for the three crosses at varying levels of k are highly significant in all but two cases (Table 2). The exceptions are observed for k = 2 in crosses of SJC-1 × S5971, which is significant at $P < 0.05$, and SJC-1 × DPL 70, which is not significant. Examination of individual χ^2 components for generations of SJC-1 × S5971 show that significance is primarily due to a lack of fit in back-cross and F_3 generations. In the SJC-1 × 4-42 cross, F_1, F_2, and F_3 generations are primarily responsible for the lack of fit. Clearly, a single-locus model for the control of *Verticillium* wilt tolerance is not consistent with progeny distributions for SJC-1 × S5971 or SJC-1 × 4-42.

Table 1. Expected cell probabilities for the j^{th} interval assuming single-locus segregation

Subscript	Generation	*P*
1	P_1	α_{0j}
2	B_1	$1/2\ (\alpha_{0j} + \alpha_{1j})$
3	F_1	α_{1j}
4	F_2	$1/4\ (\alpha_{0j} + 2\alpha_{1j} + \alpha_{2j})$
5	B_2	$1/2\ (\alpha_{1j} + \alpha_{2j})$
6	P_2	α_{2j}
7	F_3	$1/8\ (3\alpha_{0j} + 2\alpha_{1j} + 3\alpha_{2j})$

The SJC-1 × DPL 70 cross is the only case where an adequate fit for a single-locus model was observed, and this occurred only for k = 2. For values of k > 2, the χ^2

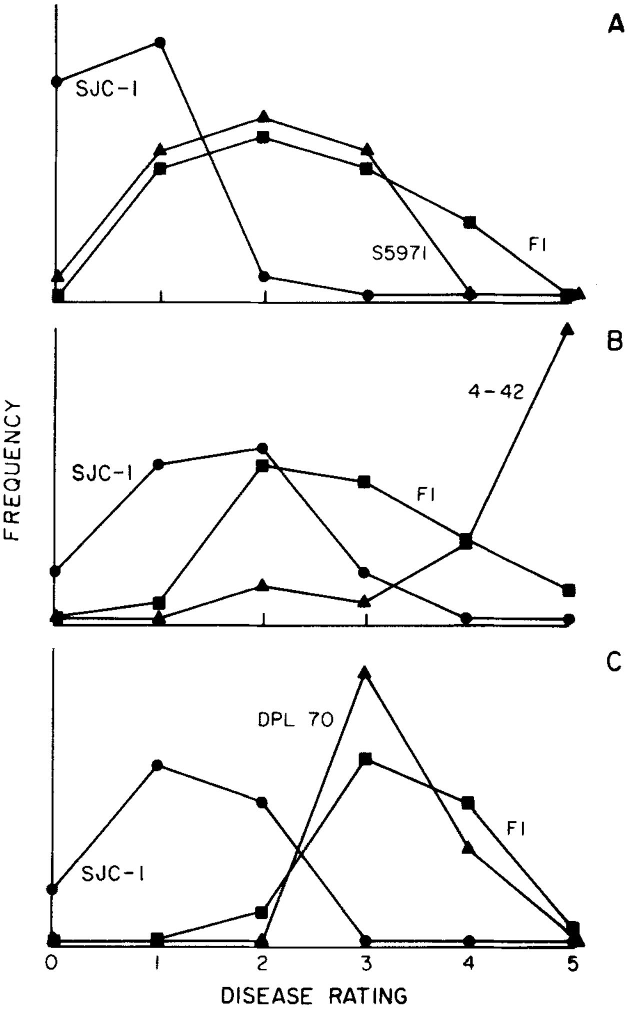

Fig. 1 A–C. Frequency distributions of *Verticillium* wilt tolerance in parental and F_1 generations for crosses **A** SJC-1 × S5971; **B** SJC-1 × 4-42; **C** SJC-1 × DPL 70

Table 2. Chi-square statistics for one-locus segregation model of *Verticillium* wilt tolerance in generations derived from three cotton crosses

Generation	No. of intervals (k)				
	2	3	4	5	6
	Acala SJC-1 × S5971				
P_1	0.02	0.10	0.03	0.68	3.57
B_1	2.14	9.52**	6.16	5.53	25.21**
F_1	2.48	1.01	3.24	1.61	1.52
F_2	0.85	0.86	1.10	1.03	1.89
B_2	0.01	9.83**	7.38	9.61*	24.57**
P_2	0.18	3.63	2.93	2.58	7.19
F_3	5.25*	23.93**	18.39**	16.28**	25.07**
Total	10.93*	48.88**	39.25**	37.34**	89.01**
	Acala SJC-1 × Acala 4-42				
P_1	1.13	5.98	5.18	11.61*	69.90**
B_1	6.64**	7.55*	7.24	4.83	5.48
F_1	0.12	14.13**	23.69**	43.33**	7 160.36**
F_2	16.26**	21.04**	17.59**	16.87**	21.53**
B_2	0.10	3.97	2.59	3.64*	12.36*
P_2	0.15	1.60	5.81	12.14*	17.80**
F_3	10.65**	3.62	19.00**	9.90*	20.08**
Total	35.06**	57.89**	81.10**	102.31**	7 306.51**
	Acala SJC-1 × Deltapine 70				
P_1	0.00	92.63**	109.96**	108.36**	87.41**
B_1	0.07	1.06	0.38	3.70	2.98
F_1	0.68	0.80	0.93	2.31	2.33
F_2	1.60	8.52*	13.09**	5.12	25.86**
B_2	0.43	3.26	3.49	5.26	10.77
P_2	0.08	2.51	0.67	0.71	4.11
F_3	1.58	14.49**	6.44	8.94	14.39*
Total	4.45	123.26**	134.95**	134.41**	147.84**

*, ** Significant at the 0.05 and 0.01 probability level, respectively

test statistics are generally greater than those for SJC-1 × S5971 or SJC-1 × 4-42. We therefore conclude that even in this cross, the genetic control of inheritance to *Verticillium* wilt tolerance appears to be more complex than expected from the segregation of one genetic factor. Further breeding tests and the methods of maximum likelihood (Elston and Stewart 1973) are necessary to evaluate alternative models of inheritance.

Chi-square tests have some limitations, among which is that the expected cell probabilities should not be too small (Hole 1984). As the arbitrary number of intervals increases, there is a tendency for the χ^2 to become spuriously high due to low cell probabilities. For example, the χ^2 value for $k=6$ in SJC-1 × 4-42 is spuriously high although obviously a poor fit, where in one cell $x_{ij}=7$ and $n_i p_{ij}=0.0068$. A few other χ^2 values appeared to be inflated in these data; however, if the contribution from cells with low expected probability was subtracted from the total χ^2, the statistic was still significant in every case.

If the expected frequency of a cell is too small, say < 3, this cell should be combined with one or more other cells to increase the frequency. However, with fewer degrees of freedom, the χ^2 test lacks power. The optimim level of k is the highest value for which there are no cells with spuriously high contributions to χ^2. Therefore, it is important to repeat the test for varying levels of k.

The minimum χ^2 technique applied here does not require a recursive numerical solution or assumptions of normality and homoscedasticity as in parametric maximum likelihood methods (Elston and Stewart 1973). However, the present method is not easily extended to an arbitrary number of loci (Elston 1981). This is because for a trait controlled by two or more loci, new genotypes, not present in the parental and F_1 individuals, may appear in backcrosses, F_2s and F_3s. Without making specific assumptions about the form of the phenotypic distributions, the data will automatically fit expected distributions perfectly. Also, for the present study we would need evaluations on a greater number of individuals and a more sensitive method of evaluation to detect these new genotypes.

Generation means analysis

Genetic effects for quantitative characters may be estimated from an analysis of generation means as described by Hayman (1958). The use of this analysis is based upon assumptions that the parents are homozygous, genotype × environment interactions are not significant, tolerance genes which are different are associated in one parent, and that there is linkage equilibrium for the epistatic models.

Variation among generation means for tolerance to *Verticillium* wilt was highly significant in all crosses. A summary of means, genetic parameters, and a test for goodness of fit of the models is presented in Table 3. The outcome of these analyses shows that the additive-dominance model is adequate for the crosses of SJC-1 × S5971 and SJC-1 × DPL 70, but inadequate for SJC-1 × 4-42. Additive effects were negative (since P_1 was the low parent) and highly significant for SJC-1 × S5971 and SJC-1 × DPL 70, as judged by a *t*-test. Dominance effects were positive and significant for SJC-1 × S5971 and positive and highly significant for SJC-1 × DPL 70. A positive value for dominance indicates that genes for tolerance are generally recessive in these crosses, as was observed in Fig. 1A and C. Recessiveness for tolerance to *Verticillium* wilt in cotton has been observed in other studies as well (Barnes and Staten 1961; Devey 1986; Roberts and Staten 1972).

Table 3. Mean ratings and estimation of genetic effects for *Verticillium* wilt tolerance in three cotton crosses

Generation	SJC-1×S5971	SJC-1×4-42	SJC-1× DPL 70
	Means		
P_1	0.593	1.519	1.222
B_1	1.389	2.519	2.648
F_1	2.296	2.889	3.370
F_2	1.574	2.259	3.148
B_2	1.741	3.370	3.444
P_2	1.926	4.519	3.259
F_3	1.611	3.167	2.759
Parameter	Genetic effects		
m	1.661±0.071	2.740±0.372	2.966±0.071
a	−0.603±0.096	−0.772±0.916	−0.949±0.103
d	0.896±0.208	−0.177±1.645	1.212±0.205
aa	–	0.085±1.496	–
ad	–	0.732±1.076	–
dd	–	0.699±3.550	–
χ^2	4.58	22.80	8.62
P	0.50 −0.25	>0.005	0.10 −0.05

Table 4. Heritability estimates for *Verticillium* wilt tolerance in two crosses computed using regression of actual and standardized data, and 10% selection (realized)

Method	SJC-1×S5971	SJC-1×DPL
Actual	0.149**	0.222**
Standard unit	0.275**	0.262**
Realized	0.123	0.215*

*, ** Significant at the 0.05 and 0.01 probability level, respectively

A diallel study including, among others, the four genotypes used here showed significant specific combining ability effects for the crosses of SJC-1×S5971 and SJC-1×DPL 70 (Devey 1986). The sca effects, which include dominance and certain types of epistasis, were not common among the other crosses. Therefore, while dominance may be important in some cases, it is probably not expected.

For the SJC-1×4-42 cross, a satisfactory fit could not be obtained even when all six parameters were included in the model. This is shown by the significant χ^2, which is the residual error sum of squares in a weighted regression analysis. Due to significant lack of fit, none of the parameters except m were significant. It was noted that levels of susceptibility in 4-42 were considerably higher than observed in previous years when the cultivar was included in other studies (Devey and Rosielle 1986), suggesting genotype×environment interaction.

Failure of the SJC-1×4-42 cross to fit the digenic epistatic model (m, a, d, aa, ad, and dd) may also indicate either the presence of trigenic epistasis or linkage or both (Hayman 1958). In the F_2-metric used here, all estimates are linkage biased when linkage occurs among interacting genes (Van der Veen 1959). The absence of epistatic effects and a non-significant χ^2 for crosses of SJC-1×S5971 and SJC-1×DPL 70 suggest that trigenic epistasis and linkage were not important factors in these analyses.

Heritabilities

Estimates of heritability for the crosses of SJC-1×S5971 and SJC-1×DPL 70 are presented in Table 4. The standard unit heritability (Frey and Horner 1957) differs little from estimates based on actual values, indicating that a particular type of genotype×environment interaction which causes inflated heritability estimates did not occur. This "expansion effect" may result from parents and offspring being grown in different environments. Realized heritability estimates agree closely with the other two estimates.

Presumably, the low heritabilities are a result of individual plant selection in the F_2 and environmental influences on the trait. Roberts and Staten (1972) reported that regression of progeny wilt grades on F_2 plants gave much lower heritabilities than by other methods. They attributed this to about 10% of the F_2 plants which escaped disease effects and were not detected as susceptible until progeny tested.

In another study (Devey 1986) based on replicated F_1 and F_2 progeny evaluations in a diallel cross analysis, narrow-sense heritability estimates were 0.61 and 0.69, respectively. The higher estimates are probably related to circumstances under which the values were determined – replicated progeny tests in the same year. Based on these, and results of Roberts and Staten (1972), individual plant selection does not appear to be an efficient method of selection for *Verticillium* wilt tolerance, although under high selection intensity, genetic gains are still possible.

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