INHERITANCE OF RESISTANCE OF 'SALINAS 88' LETTUCE TO THE ROOT-KNOT NEMATODE Meloidogyne incognita (Kofoid & White) Chitwood.

HERANÇA DA RESISTÊNCIA DA ALFACE 'SALINAS 88' AO NEMATÓIDE DAS GALHAS MELOIDOGYNE INCOGNITA (KOFOID & WHITE) CHITWOOD.

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RESUMO

Este estudo observou o modo de herança da resistência da alface 'Salinas 88' ao nematóide das galhas *Meloidogyne incognita* raça 1 (Kofoid & White) Chitwood. Os tratamentos envolveram as linhas parentais 'Regina 71' (P_2, suscetível) e 'Salinas 88' (P_1, resistente), assim como as gerações $F_1(P_1xP_2)$ e $F_2(P_1xP_2)$. O experimento foi conduzido em delineamento em blocos casualizados com cinco repetições. Foram avaliadas plantas individuais com uma escala de notas de 1(=resistente) a 5(=suscetível), 45 dias após a inoculação com o patógeno, de cada planta foi avaliada a nota para número de galhas (GNS), nota para massas de ovos (ENS) e incidência de galhas (OGI) por sistema radicular. A hipótese de herança monogênica não foi rejeitada (até o limite de significância do χ^2) para OGI e GNS, indicando que a resistência pode estar sob controle de um único locus gênico. Resultado divergente foi encontrado para o teste de χ^2 para ENS, em que a hipótese de herança monogêncida foi rejeitada. Isso indica que se em 'Salinas 88' existe a presença de um gene para a resistência ao nematóide, ele pode está sendo influenciado pela presença de genes modificadores adicionais. O teste de máxima verossimilhança evidenciou a presença de um gene maior com dominância parcial (na direção de maior nível de resistência) e a ação de genes modificadores.

Palavras chave: *Lactuca sativa* L., herança, herdabilidade, nematóide das galhas.

ABSTRACT

This study looked into the inheritance mode of resistance of 'Salinas 88' lettuce to the root-knot nematode *Meloidogyne incognita* race 1 (Kofoid & White) Chitwood. The treatments involved the parental lines 'Regina 71' (P2, nematode susceptible) and 'Salinas 88' (P1, nematode resistant), as well as the $F_1(P_1xP_2)$ and $F_2(P_1xP_2)$ generations. The experiment had a randomized complete block design with five replications. Altogether, 37 plants from 'Regina 71', 40 from 'Salinas 88', 40 from the F_1 generation and 181 from the F_2 generation were evaluated. Individual plants were evaluated with a score grades from 1(=resistant) to 5(=susceptible), 45 days after infestation with the pathogen, for gall number scores (GNS), eggmass number scores(ENS), and overall gall incidence (OGI) on the root system. Broad-sense heritabilities for GNS, ENS and OGI were estimated at 16.3%, 57.4% and 21.5%, respectively. The estimates of the mean degrees of dominance indicated partial dominance in the direction of a higher resistance. The monogenic hipothesis of inheritance was not rejected (at the limit of χ^2 test significance) for OGI and GNS, indicating that that resistance may be under control of a single gene locus. Divergent χ^2 tests performed for ENS rejected the hipothesis of monogenic inheritance, indicating that, if a major gene for nematode resistance is present in 'Salinas-88', its action may be influenced by the action of additional modifier genes. The test of maximum likelihood provided evidence both for the presence of one major gene with with partial dominance (in the direction of higher levels of resistance) and for the action of modifier polygenes.

Key words: *Lactuca sativa* L., inheritance, heritability, root-knot nematode.

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(Recebido para Publicação em 16/05/2007, Aprovado em 15/05/2008)

INTRODUCTION

In the Brazilian market lettuce ranks first among the leafy vegetables of greatest consumer demand. Butterleaf types are preferred, and comprise 54% of the total 26407 metric tons marketed at CEAGESP, the country´s leading horticultural distribution centre.

A great deal of effort has been dedicated in Brazil to lettuce genetic improvement, in order to create cultivars that are better adapted to the country's tropical conditions, especially those that associate heat tolerance (slower bolting at temperatures > 25^{o} C) and resistance to lettuce mosaic virus (LMV). One of the critical problems yet to be solved are the root knot nematodes of the genus *Meloidogyne* spp. Root knot nematodes cause considerable lots to a wide range of vegetable crops, and their control is difficult due to the large number of host plant species and to their great capacity of survival under a wide range of edaphoclimatic conditions. The nematodes have a short life cycle (28-70 days) and are highly prolific (2.000-2.850 eggs/female). Large egg populations are accumulated in the soil after consecutive crops of species considered good hosts (CAMPOS et al., 2001). The sedentary endoparasitic nematodes damage the root system and impair water and mineral salt uptake, affecting commercial characteristics, such as leaf color, head formation, plant size and weight. Lettuce cultivars under attacked by nematodes become atrophied and yellowish, which disqualifies them for sale (CAMPOS, 1985).

One of the most common practices in the phytonematode control of the root-knot in several crops is the use of chemical products, which are however highly toxic, with long residual half-lives which lead to health and environmental problems. The use of resistant cultivars of diverse horticultural species has become an important alternative in the control of this pathogen.

Genetic resistance is considered one of the most effective methods for the control of root-knot nematodes (*Meloidogyne spp.*) (MALUF, 1997). In the case of lettuce, relatively few reports of resistance have been made. CHARCHAR & MOITA (1996) evaluated 45 lettuce cultivars of different types and verified that 10 presented a certain resistance level (all looseleaf types with heavily fringed leaves). Major tolerance in fringed looseleaf cultivars was also observed by GOMES (1996) and MENDES (1998). Other studies (MALUF et al., 2003; WILCKEN et al., 2005) reported that 'Salinas 88', a USDA crisphead cultivar, presents resistance to *M. incognita* as well as to *M. javanica*. Nematode resistance in smooth leaved (butterleaf) types has not yet been reported.

Studies of inheritance for *Meloidogyne* resistance, performed with crosses between the cultivars Regina 71 (susceptible, smooth leaves) and Grand Rapids (resistant, fringed leaves), evidenced so far that both for *M. incognita* (GOMES, 1999) and for *M. javanica* (MALUF et al., 2002), the trait is controlled by a single gene locus, in which the allele responsible for the resistance was tentatively denominated *Me* (GOMES et al., 2000). The studies also showed that nematode resistance had a predominantly additive gene action, with a relatively high broad-sense heritability, which should favour the selection of new resistant cultivars and breeding lines.

Knowledge about the genetic control of the resistance to root-knot nematodes in other lettuce cultivars of different types becomes increasingly important as new possibilities in improvement programs come up. Other desirable characteristics present in genotypes resistant to root-knot nematodes, as in the case of LMV resistance of the crisphead cultivar Salinas 88 (STANGARLIN, 1997), can easily be integrated into these programs. The objective of the present study was therefore to study the mode of inheritance of resistance in the cultivar Salinas 88 to root-knot nematode *M. incognita* race 1 (kofoid & White) Chitwood.

MATERIALS AND METHODS

The experiment was performed in a greenhouse at the HortiAgro Seeds Ltda., in the county of Ijaci, MG, Brazil. The county lies in the southern region of the state of Minas Gerais (21°10' S, 44°55' W, approximately 832 m altitude). The mean annual temperature is 19.4°C, with lowest monthly means of 14.8°C and highest means of 26.1°C. The experiment was conducted between 16/10/2005 and 16/12/2005, when temperatures oscillated between 22°C and 28°C.

Inheritance was studied in crosses between letucce cultivares Regina 71 and Salinas 88. Regina 71, a Brazilian cultivar with smooth loose leaves, is highly resistant to early bolting, but is susceptible to *M. incognita* race 1. Salinas 88, a USDA crisphead cultivar, is resistant to *M. incognita* (MALUF et al., 2003 & FERREIRA et al., 2005) as well as to

M. javanica (FERREIRA et al., 2005). The parental cultivars Regina 71 and Salinas 88, their F_1(Salinas 88 x Regina 71) and F_2(Salinas 88 x Regina 71) generations were tested for nematode resistance. The experimental design was of randomized blocks with five replications. Altogether, 37 plants Regina 71, 40 of Salinas 88, 40 the F_1 and 181 of the F_2 generation were tested.

Seeds were sown on Styrofoam trays of 128 cells (approximately 44 cm^3 per cell) filled with commercial Plantmax® substratum. Two to three seeds were sown per cell and, after germination, at the first adult leaf stage, the seedlings were thinned to only one plantlet per cell. On each tray, one row (eight plants) was sown with tomato cultivar Santa Clara, susceptible to *Meloidogyne* spp., in order to check for the viability of the inoculum, through the confirmation of gall formation on the tomato plants roots just before the period of evaluation. Fifteen days after sowing, the substrate was infested with 1320 eggs of an isolate *M. incognita* race 1, by injecting a suspension of eggs beside each plant, directly into the substratum (GOMES et al., 2000). The eggs were extracted by a technique proposed by HUSSEY & BARKER (1973), modified by BONETTI & FERRAZ (1981), and were obtained from *M. incognita* race 1 isolates maintained in nematode susceptible 'Santa Clara' tomato plants grown in 10 dm^3 pots, kept in a greenhouse at the University Federal de Lavras/ Lavras-MG campus.

Forty-five days after inoculation, the tomato plants were removed from the trays. An intense formation of galls and egg masses on the roots was verified, confirming the inoculation efficacy. Each lettuce plant was then evaluated individually for their response to nematode inoculation.

The plants were removed from the trays and evaluated, with the root ball intact, for overall gall incidence (OGI) on the root system. For this trait, the root system of each plant was visually evaluated and graded, according to FIORINI et al. (2005):

grade 1 = root systems with few visible galls (<10 galls), small (up to 1 mm) and non-coalescent;

grade 2 = root systems with few visible galls (<10 galls), though some with intermediate size (1mm to 3mm);

grade 3 = root systems with a intermediate number of visible galls (10-30 galls), of intermediate size and some of large size (> 3mm);

grade 4 = root systems with many visible galls (> 30 galls), predominantly with large size (> 3mm), with few galls of intermediate size; some galls coalescent,

grade 5 = root systems with many visible, large galls (> 30), with a high number of coalescent galls.

For the traits grade for number of galls and grade number of egg masses, the plant root systems were submerged in water to loosen the substrate from the root ball. The roots were carefully washed clean of any substratum in standing water and immediately stained with a dye used in the food industry, containing 1% Bordeaux (ROCHA et al, 2005), to visualize the egg masses. The number of galls and egg masses per root system were then counted and graded accordingly.

The following 1 to 5 grade scale was used to assess eggmass number scores (ENS): number of galls ≤ 20 = score 1; > 20 and ≤ 40 = score 2; > 40 and ≤ 60 = grade 3; > 60 and ≤ 80 = grade 4; > 80 = grade 5. An analogous 1 to 5 grade scale was used to assess gall number scores (GNS): score 1 = number of egg masses ≤ 10; score 2 = number of egg masses > 10 and ≤ 20; score 3 = number of egg masses > 20 and ≤ 30; score 4 = number of egg masses > 30 and ≤ 40; score 5 = number of egg masses > 40. Thus, score 1 characterized plants with greatest resistance, while score 5 identified plants with highest susceptibility.

Means and variances of GNS, ENS and OGI were estimated for each of the populations in each trial. Genetic (σ^2_G), environmental (σ^2_E) and phenotypic variances ($\sigma^2_{F_2}$), broad-sense heritability (H^2) were calculated (Ramalho, Santos & Zimmermann, 1993). The mean additive [a] and non-additive effects [d] of the gene (s) that control(s) each trait were estimated based on the generation means, by the method of the weighted least squares (MATHER & JINKS, 1977). Thereafter, the the mean degree of dominance (MDD) was estimated (MDD= [d]/[a]).

Test of hypothesis of monogenic inheritance

The data observed in the different generations were used to verify the hypothesis of monogenic inheritance, under different mean degrees of dominance assumed (GOMES et al., 2000; Oliveira et al., 2003 & MENEZES et al., 2005). This

hypothesis was tested under different mean dominance degrees, considering the following presuppositions:

a) data distribution for each of the generations (P_1, P_2, F_1 and F_2) were assumed to have a normal distribution;

b) A truncation point (TP) was established, below which were located most of the resistant P_1 (Salinas 88) plants and above which were most of the susceptible P_2 (Regina 71) plants. The TP chosen was a score of 2, for all traits under study (GNS, ENS, OGI).

c) for each one of the parental generations, the true mean ($\overline{P_1}, \overline{P_2}$) was considered equal to the expected respective mean and the true variance equal to the estimated respective variance;

d) Based on a normal distribution, the expected frequencies of P_1 and P_2 plants equal to or lower than the TP were estimated.

e) the mean of the F_1 generation was admitted as:

$$\overline{F_1} = \frac{(\overline{P_1} + \overline{P_2})}{2} + DD \cdot \frac{(\overline{P_2} - \overline{P_1})}{2}$$, where DD is the presumed degree of dominance under consideration; and $\overline{P_1}$ and $\overline{P_2}$ are the means of the respective parental lines. The true variance for the F_1 population was admitted as equal to the respective estimated variance. With the mean and variance of the F_1 population, the expected frequency of F_1 plants with scores ≤ TP was estimated.

f) given the hypothesis of monogenic inheritance, for F_2 an expected frequency of the number of plants with mean ≤ TP was calculated as being the weighted mean of the expected frequencies in P_1, F_1 and P_2, with weights of 1:2:1, respectively;

g) the expected plant frequencies with mean ≤ TP obtained for P_1 (item d), P_2 (item d), F_1 (item e) and F_2 (item f) were multiplied by the number of plants evaluated per generation to obtain the expected number of plants with mean ≤ TP under the hypothesis of monogenic inheritance with the DD considered;

h) the expected numbers of plants in P_1, P_2, F_1 and F2 with means ≤ TP were compared to the effectively obtained numbers, computing the chi-square value with two degrees of freedom (since the P_1 and P2 frequencies were summed up in one category, due to the zero value of the expected frequency of P_2 for the GNS trait).

i) significance of the obtained chi-square value implies in rejection of the hypothesis of monogenic inheritance under the considered dominance degree. On the other hand, the non-significance of the obtained chi-square value (χ^2) results in non-rejection of this hypothesis, admitting the possibility of dealing with monogenic inheritance under the DD considered.

Tests of genetic models using the maximum likelihood function

Parameters related to the effect of a major genes plus polygenes will be estimated through the maximum likelihood function, according to the methodology proposed by SILVA (2003): based on the mean and variance components (MATHER & JINKS, 1977), the data distribution was considered normal, as shown below:

$$P_1 : N(\mu - [a] - A, \sigma^2)$$

$$P_2 : N(\mu + [a] +, \sigma^2)$$

$$F_1 : N(\mu + [d] + D, \sigma^2)$$

$$F_2 : \frac{1}{4}N\left(\mu + \frac{[d]}{2} - A, \sigma^2 + V_A + V_D\right) + \frac{1}{2}N\left(\mu + \frac{[d]}{2} + D, \sigma^2 + V_A + V_D\right) + \frac{1}{4}N\left(\mu + \frac{[d]}{2} + A, \sigma^2 + V_A + V_D\right)$$

where: μ = constant of reference; A = additive effect of gene of major effect ; D = dominance effect of gene of major effect ; $[a]$ = polygenic additive component; $[d]$ = polygenic component of dominance; V_A = additive variance of the polygenic gene effects; V_D = variance attributed to the

dominance deviations the polygenic effects and σ^2 = environmental variance.

The density function for F_2 consisted of a mixture of three normal distributions, where, in each component of the mixture, the mean components of variance of polygenes do not change, unlike the effects of the gene of major effect. All parameters were estimated by the use of the method of maximum likelihood and diverse genetic models were constructed (Table 1).

Table 1. Inheritance models tested for resistance to *M. incognita* with the method of maximum likelihood.

Models	Parameters
1= major gene with additive and dominance effect + polygenes with additive and dominance effect	μ, A, D, [a], [d], V_A, V_D, S_{AD}, σ^2
2= major gene with additive and dominance effect + polygenes with additive effect only	μ, A, D, [a], V_A, σ^2
3= major gene with additive effect only + polygenes with additive and dominance effect	μ, A, [a], [d], V_A, V_D, S_{AD}, σ^2
4= major gene with additive effect + polygenes with additive effect only	μ, A, [a], V_A, σ^2
5= polygenes with additive and dominance effect	μ, [a], [d], V_A, V_D, S_{AD}, σ^2
6= polygenes with additive effect only	μ, [a], V_A, σ^2
7= major gene with additive and dominance effects	μ, A, D, σ^2
8= major gene with additive effect only	μ, A, σ^2
9= effect of the environment only	μ, σ^2

μ: constant of reference;
A: additive effect of the gene of major effect;
D: dominance effect of the gene of major effect;
[a]: additive polygenic component;
[d]: polygenic component of dominance;
V_A: additive variance of the polygenic effects;
V_D: dominance variance of the polygenic effects
S_{AD}: component of variation of the products of the additive polygenic effects by the polygenic effects of dominance;
σ^2: environmental variance.

The models 1, 3 and 5 could not be tested due to absence of the backcrosses $BC_{(P1)}$ and $BC_{(P2)}$, which impaired an estimation of the dominance variance associated to the polygenic effects.

The likelihood tests were carried out with the LR statistics (MODD et al., 1974):

$$LR = -2\ln\frac{L(M_I)}{L(M_J)}$$

where L(Mi) and L(Mj) are the likelihood functions of the models i and j, where model i must be hierarchized to model j. The tests were performed using the statistical software package Monogen v.0.1 (SILVA, 2003).

RESULTS AND DISCUSSION

The means of the F_1 and F_2 generations were intermediate to the means of the parental lines for GNS, ENS and OGI (Table 2). The estimate of broad-sense heritability was relatively high for GNS (57.4%) and lower for ENS (21.5%) and OGI (16.3%). The phenotypic variance was similar for the three traits under study. The lower values for broad-sense heritabilities of ENS and OGI indicate that these traits are more influenced by the environment than GNS. The values found for broad-sense heritability of GNS indicate that superior individuals could be effectively selected from segregating population using this criterion. GOMES et al. (2000) studied the inheritance of *M. incognita* resistance of cultivar Grand Rapids and found values of broad-sense heritability of 68.3% and 72.5% for the traits number of galls and number of egg masses, respectively. The difference between the values of heritability of the studies may be due the use of different resistance sources and other experimental conditions.

The estimate of the mean degrees of dominance (MDD) obtained from the least square estimates were -0.421, -0.412 and -0.764, respectively for GNS, ENS and OGI, indicating an additive-dominant model, with partial dominance in the direction of lower scores, i.e., higher levels of nematode resistance (Table 2). These values are similar to the MDD values estimated by the maximum likelihood test (Table 3).

Table 2. Estimates of the genetic and phenotypic parameters for gall number scores (GNS), eggmass number scores (ENS), and overall gall incidence (OGI) in lettuce inoculated with *Meloidogyne incognita*. UFLA, Lavras, MG, 2006.

Parameter	GNS	ENS	OGI
$\overline{P_1}$	**1.650**	**1.400**	**1.375**
$\overline{P_2}$	**4.892**	**4.108**	**3.405**
$\overline{F_1}$	**2.667**	**2.487**	**1.615**
$\overline{F_2}$	**2.801**	**2.227**	**2.000**
$\sigma^2_{P_1}$	**0.695**	**0.605**	**0.907**
$\sigma^2_{P_2}$	**0.155**	**1.044**	**1.081**
$\sigma^2_{F_1}$	**1.123**	**0.888**	**0.559**
$\sigma^2_{F_2}$	**1.160**	**1.076**	**0.978**
σ^2_{G}	**0.666**	**0.231**	**0.159**
σ^2_{E}	**0.494**	**0.845**	**0.818**
H^2	**0.574**	**0.215**	**0.163**
m	**3.208**	**2.683**	**2.389**
[a]	**1.602**	**1.398**	**1.015**

[d]	**-0.674**	**-0.575**	**-0.775**
MDD	**-0.421**	**-0.412**	**-0.764**

Where: $\overline{P_1}$ = mean of 'Salinas 88'; $\overline{P_2}$ = mean of 'Regina 71'; $\overline{F_1}$ = mean of F_1 (Salinas 88 x Regina 71); $\overline{F_2}$ = mean of F_2 (Salinas 88 x Regina 71); $\sigma^2_{P_1}$ = variance of Salinas 88; $\sigma^2_{P_2}$ = variance of Regina 71; $\sigma^2_{F_1}$ = variance of F_1; $\sigma^2_{F_2}$ = variance of the F2 population =phenotypic variance; σ^2_G = genetic variance; σ^2_E = environmental variance; H^2= broad-sense heritability; m= parental mean; [a]= additive component of the mean; [d]= dominance (non-additive) mean component; MDD= mean degree of dominance= [d]/[a].

m, [a], [d] are least square estimates

Table 3. Comparison of the mean degrees of dominance (MDD) estimated by least squares and by maximum likelihood for the traits gall number scores (GNS), eggmass number scores(ENS), and overall gall incidence (OGI) in lettuce inoculated with *Meloidogyne incognita*. UFLA, Lavras, MG, Brazil,2006.

Traits	**MDD**	
	Max. likelihood	**Least squares**
GNS	**-0.420**	**-0.421**
ENS	**-0.403**	**-0.412**
OGI	**-0.770**	**-0.764**

Based on the plant frequency of the parental lines Salinas 88 (P_1) and Regina 71 (P_2) for each grade, grade 2 was determined as truncation point (TP) for all studied traits (Figure 1). The hypothesis of monogenic inheritance, with a degree of dominance -0.8 can be admitted as valid for GNS (at limit of the significance), evidencing partial dominance of the allele that conveyed major resistance (lower GNS) (Figure 2). Likewise, for OGI, the hypothesis of monogenic inheritance can be admitted valid in a range of degrees of dominance around -1.4 (Figure 2), which would indicate overdominance − a hypothesis that is not supported by the mean components for this trait (Table 2). Since the hypothesis of monogenic inheritance is at the limit of rejection for OGI, this estimate of degree of dominance can be attributed to the presence of modifier genes (polygenes). For ENS, the hypothesis of monogenic inheritance was clearly rejected under any assumed degree of dominance, evidencing that the trait is indeed influenced by more than one gene locus (Figure 2).

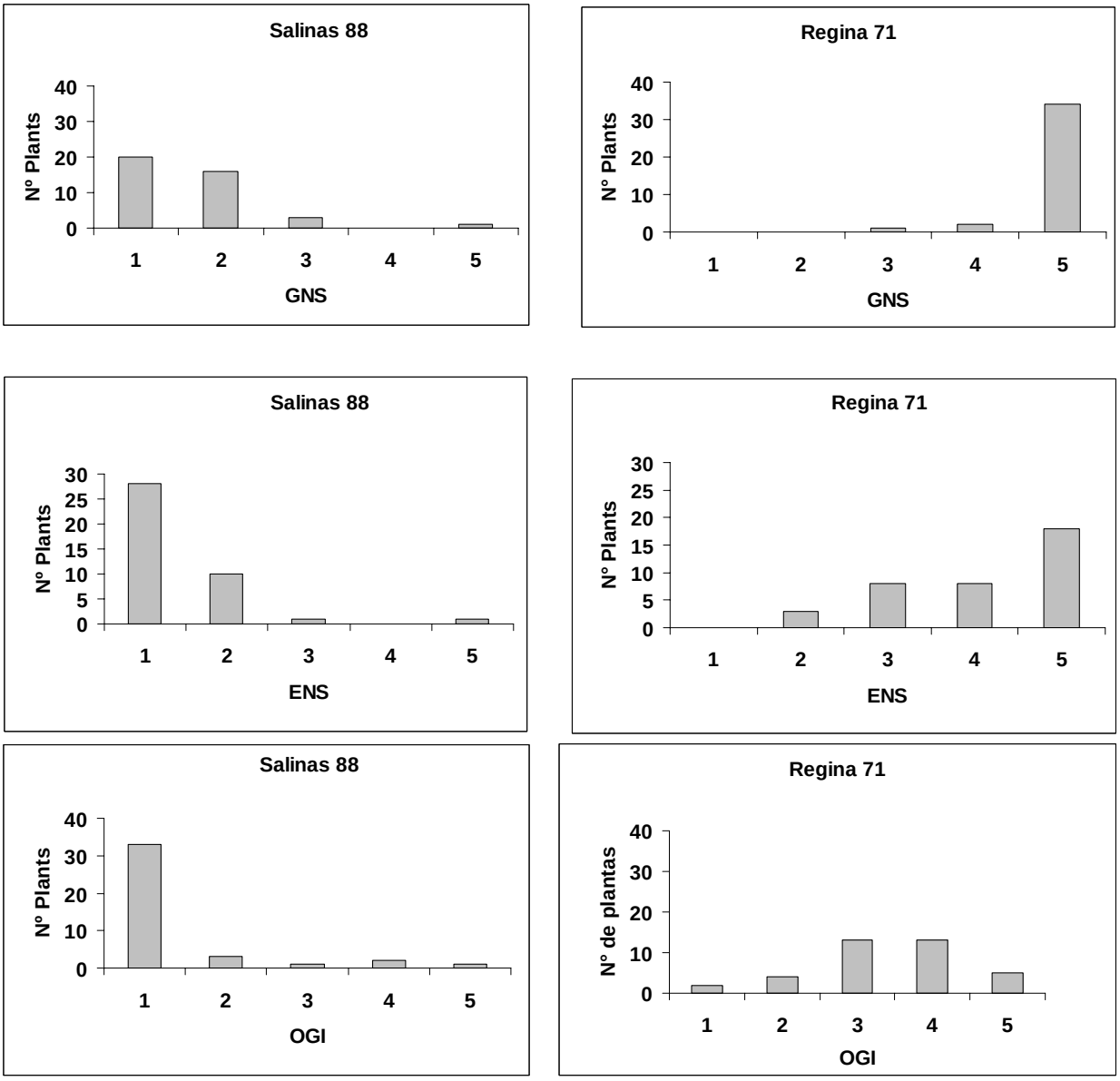

Figure 1. Frequency distributions of gall number scores (GNS), eggmass number scores (ENS) and overall gall incidence (OGI) in plants of the cultivars Salinas 88 and Regina 71. UFLA, Lavras, MG, 2006.

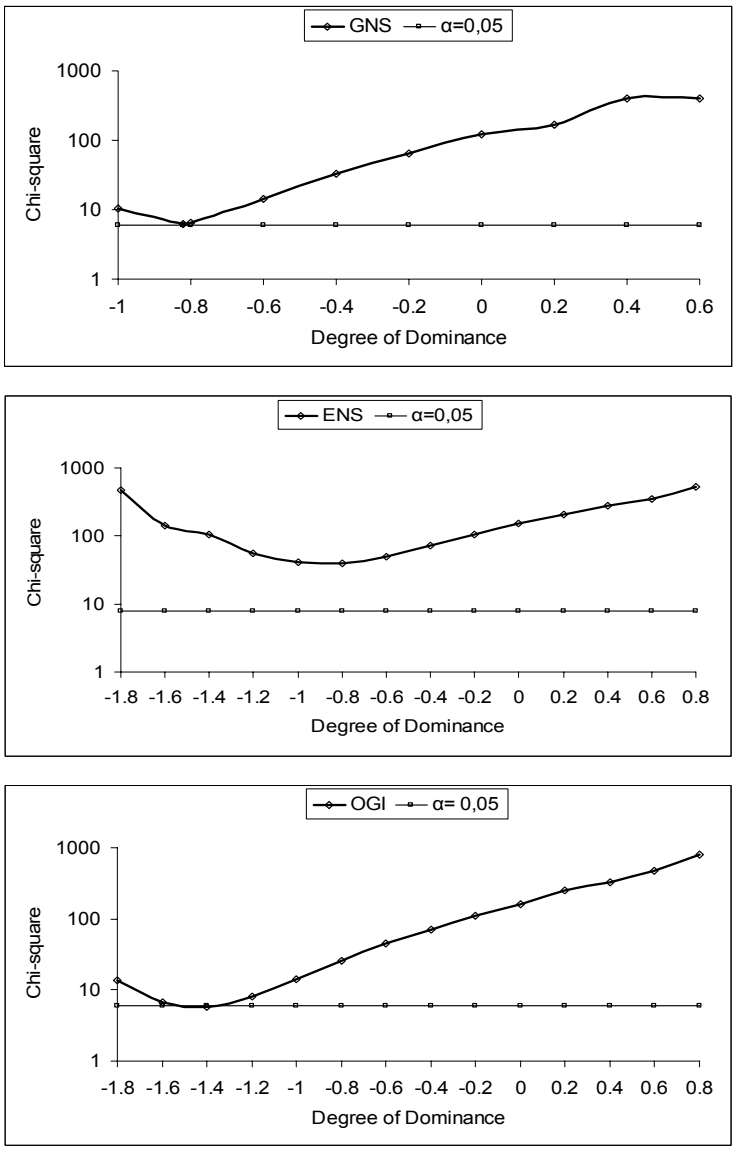

Figure 2. Chi-square tests of hypotheses of monogenic inheritance at different presumed degrees of dominance for gall number scores (GNS), for the eggmass number scores (ENS) and overall gall incidence (OGI) in lettuce inoculated with *Meloidogyne incognita*. UFLA, Lavras, MG, 2006.

Based on the tests of genetic models using the likelihood function to compare Models 7 and 9 (SILVA, 2003) for all three traits, the presence of one major gene with additive and dominance effects was evidenced (Table 4). Likewise, when comparing Models 7 and 8, the hypothesis (H_0) was rejected, indicating significant dominance effects of the major gene. When Model 2 and 7 were confronted for the trait GNS, hypothesis (H_0) was rejected, evidencing that in addition to one major gene with additive and dominance effects, there are also polygenes with additive effects that influence expression of response to the nematode. For OGI, hypothesis H_0 was not rejected in the confrontation of Models 2 and 7, evidencing that this trait could be less affected by the polygenes than GNS.

Table 4. Likelihood tests among genetic models for gall number scores (GNS), eggmass number scores (ENS), and overall gall incidence (OGI) in lettuce affected by *Meoidogyne incognita*. UFLA, Lavras, MG, 2006.

Tests	GNS	ENS	OGI
	χ^2	χ^2	χ^2
2 vs 7	14.92*	-	3.69
7 vs 8	37.85*	23.82*	29.28*
7 vs 9	181.58*	127.05*	92.53*
8 vs 9	-	16.26*	-

- negative values obtained for the LR function, maybe due to problems of convergence.

* significant values, at 5% probability.

2 vs 7- Tests significance of polygenes with additive effects acting as modifiers of one major gene.

7 vs 8- Tests the significance of dominance effects of the major gene.

7 vs 9- Tests the effect of one major gene with both additive and dominance effects.

8 vs 9- Tests the effect of one major gene with additive effects.

The results obtained for the genetic control of the resistance of 'Salinas 88' to *M. incognita* are only partly similar to those obtained in study with the lettuce cultivar Grand Rapids, where the resistance control was ascribed to a single gene locus (GOMES et al., 2000). The present results diverge, however, in that modifier genes are present in the cross of cultivar Salinas 88 with Regina 71 that were not manifested when the cultivar Grand Rapids was used as a nematode resistance source. Whether the divergence is due to the presence of modifier genes only, or also to the non-allelism of the major genes controling resistance in Salinas 88 and Grand Rapids, are hypotheses that have yet to be tested.

In a parallel study evaluating 22 families F_4 (Regina 71 x Salinas 88), derived from single F_3 plants selected for resistance to *M. incognita* race 1, we found a large number (12) of non-segregating nematode resistant families (data not shown), indicating the existence of a single major gene. Nevertheless, two families with a higher resistance level than the resistant parental line 'Salinas 88' were identified, which appears to confirm the presumed action of modifier polygenes affecting the trait expression conveyed by the major gene.

Our results therefore indicate that inheritance of the reaction of cultivar Salinas 88 to *M. incognita* race 1 is at least partly controlled by one major gene, which presents incomplete dominance in the direction of the higher resistance. The action of this major gene is modified by polygenes with lesser effects that affect the expression of resistance, and that are more clearly perceived in those traits subject to lower environmental influence (GNS).

Our results therefore indicate that inheritance of the reaction of cultivar Salinas 88 to *M. incognita* race 1 is at least partly controlled by one major gene, which presents incomplete dominance in the direction of the higher resistance. The action of this major gene is modified by polygenes with lesser effects that affect the expression of resistance, and that are more clearly perceived in those traits subject to lower environmental influence (GNS).

ACKNOWLEDGEMENTS

This study was supported by the FAPEMIG, CNPq, FAEPE, FUNDECC, Universidade Federal de Lavras and HortiAgro Sementes Ltda.

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