Determination of Resistance to *Fusarium oxysporum* in *Lilium*

Th. P. Straathof, J. Jansen, and H. J. M. Löffler

Centre for Plant Breeding and Reproduction Research (CPRO-DLO), P.O. Box 16, 6700 AA Wageningen, The Netherlands.
Paper submitted by Th. P. Straathof in partial fulfillment of requirements for a Ph.D degree. This work was financially supported by the Urgency Programme for Research on Diseases and Breeding of Flower Bulbs.
Correspondence concerning statistical analysis should be addressed to J. Jansen.
We thank H. Inggamer for technical assistance and J. M. van Tuyl and H. M. C. van Holsteijn for discussions and critical reading of the manuscript.
Accepted for publication 1 February 1993.

ABSTRACT

Straathof, Th. P., Jansen, J., and Löffler, H. J. M. 1993. Determination of resistance to *Fusarium oxysporum* in *Lilium*. Phytopathology 83:568-572.

A screening test for determination of resistance to *Fusarium oxysporum* f. sp. *lilii* in *Lilium* was developed. Under standardized conditions, 16 Asiatic lily cultivars were tested for resistance. Disease rating data were analyzed statistically using a threshold model for ordered categorical data. Bulb weight measurements were modeled as weight change of plants cultivated in *Fusarium*-infested soil relative to weight change of control plants, and further analyzed by ANOVA. Results of both observations were highly correlated. For disease ratings, six categories provided more information than two or three categories. Variation in resistance among the cultivars was demonstrated. The threshold analysis with six categories showed at least four groups of cultivars that differed in resistance. Disease ratings provided reproducible results and a practical experimental design.

Additional keywords: relative weight change, scale bulblets.

Lily (*Lilium* L.) is cultivated worldwide as a cut flower, pot plant, and garden plant. Lily bulbs are propagated vegetatively by inducing development of scale bulblets. Scale bulblets are grown for 1 or 2 yr to obtain commercial bulbs. The culture of lily bulbs, especially at the scale bulblet stage, is often limited by the soilborne fungus *Fusarium oxysporum* f. sp. *lilii* Imle (8), which causes basal rot. Infection of the bulbs leads to brownish or black necrotic lesions, and, if the whole basal plate rots, the bulbs disintegrate (3,8).

Prevention of such damage depends mostly on chemical disinfestation of soil and plant material (1,2,5,17). Resistance of the fungus to fungicides can occur (4,7), however, and reduced application of chemicals is desirable to limit environmental pollution. Another way of controlling the disease would be the cultivation of resistant cultivars, which must be developed in breeding programs. In the *Fusarium*-lily interaction, only partial resistance has been reported (8,12,14,19,20). Therefore, a standardized screening test with sufficient sensitivity to discriminate between different resistance levels is needed.

Such a test requires that observations reflect the 'true' level of resistance in the plants considered. Furthermore, for a precise quantification of differences in resistance level, the observations must be analyzed statistically. This paper describes an approach to the analysis requirement.

Often the development of symptoms is considered a reflection of susceptibility. Usually, severity of symptoms is observed visually, and results are recorded as ratings on an ordinal scale. Consistent ratings may be difficult to achieve, however, especially between experiments. Moreover, analysis of disease ratings is not straightforward because the measurement scale may be nonlinear. A threshold model for ordered categorical data (9,10,15) may provide a suitable method for analyzing disease ratings of basal rot in lily.

The difficulties associated with subjective observations may be avoided by a method to determine the decay of plants quantitatively. In this respect, weight change of plants infected by the pathogen relative to weight change of control plants may be used. Analysis of variance (ANOVA) may then be used to analyze the data.

Classification of cultivars with respect to resistance may provide a concise representation of the results of a screening test. The problem of classification of cultivars has been considered for quantitative data (6) and similar ideas can be applied in the case of disease ratings.

The aim of this paper is to compare resistance levels of scale bulblets of Asiatic lily cultivars based on disease rating data with those based on relative weight change data. Effects of combining categories on the analysis of disease ratings were considered, and cultivars were classified in groups representing different levels of resistance.

MATERIALS AND METHODS

Plant material. Cultivars were chosen so that variation in resistance level could be expected (J. M. Van Tuyl, *personal communication*). The experiment was conducted twice (in 1989 and 1990). Commercial bulbs, which were used to induce scale bulblets in the 1989 experiment, were obtained from several growers. Bulbs used in the 1990 experiment were cultivated under standardized conditions and without fungicides. Scales of commercial bulbs of 16 Asiatic lily cultivars (Aristo, Connecticut King, Enchantment, Esther, Golden Melody, Hilde, Milano, Mont Blanc, Montreux, Napoli, Orlito, Pirate [1990 experiment only], Prominence, Snow Star, Sterling Star, and Yellow Blaze) were incubated at 25 C in plastic bags with wet vermiculite to induce development of scale bulblets (21). After 8 wk at 25 C, the temperature was reduced to 17 C for another 4 wk, followed by 8 wk at 5 C. After the final incubation, newly formed scale bulblets were harvested and selected for uniformity of weight within each genotype. The resistance tests were then performed on the selected scale bulblets.

Fungus. Two highly aggressive isolates of *F. o. lilii* (CPRO-Fo14 and CPRO-Fo111) (12,13) were used. These isolates are monospore cultures provided by the Bulb Research Centre (LBO, Lisse, NL) and were stored on Protect Bacterial Preservers (Technical Service Consultants LTD, Lancs, UK) at −80 C for long-term preservation. Before experimental use, fresh cultures were obtained by plating this stock on Czapek-Dox agar medium (Oxoid LTD, Hampshire, UK). For soil infestation, the fungus was incubated for 3 wk at 23 C in an autoclaved (120 C, 2 h) oatmeal-soil mixture (1:5, w/w). The fully grown cultures were

ground and mixed in a 1:100 ratio with soil (12). The number of propagules was determined by plating soil dilutions on a modified Komada medium (11,12) immediately after mixing (±150,000 propagules per gram of soil) and at the time of planting the scale bulblets, 2 wk after infestation of the soil (±100,000 propagules per gram of soil).

Experimental design. Scale bulblets were planted in pots and placed in a temperature-controlled greenhouse at 18/14 C (16 h day/8 h night). Each pot contained four bulblets of the same genotype. The experiment was arranged in 10 blocks each of an infested and a noninfested (= control) pot of each genotype. The 16 cultivars and the two treatments were randomly assigned to the pots. Observations were made 6 (1989) or 8 (1990) wk after bulblets were planted.

Disease measurement. Disease severity was measured in two ways. Decay of the infested bulblets was rated visually according to an ordinal scale with six categories: 1 = healthy; 2 = slightly rotten; 3 = moderately rotten; 4 = heavily rotten; 5 = very heavily rotten; and 6 = completely decayed. In addition, fresh weight of each plant (bulb + stem + leaves) was measured. Roots were removed to avoid inclusion of soil particles in the weight measurements.

Analysis of ordinal data. Disease rating data were analyzed according to a threshold model for ordered categorical data (9,15). The threshold model assumes the presence of an underlying, continuous variable y that is related to disease resistance. The value of y of bulblet k (= 1...4) of cultivar j (= 1...16) in block i is given by

$$Y_{ijk} = \mu + \beta_i + \gamma_j + e_{ij} + e_{ijk}$$

where μ is the grand mean, β_i is the effect of block i ($\beta_1 = 0$), γj is the effect of cultivar j ($\gamma_1 = 0$), e_{ij} is a random contribution related to the pot with cultivar j in block i and e_{ijk} is a random contribution related to bulblet k in the pot with cultivar j in block i. The random contributions e_{ij} and e_{ijk} are assumed to be independent and normally distributed with zero mean and variances σ_P^2 and σ_B^2, respectively. The variances σ_P^2 and σ_B^2 represent between-pot and within-pot variation, respectively. The disease severity score (DSS) of cultivar j is defined as $\mu + \beta_. + \gamma_j$ where $\beta_. = \Sigma_i \beta_i / 10$, i.e., the average value for cultivar j on the underlying scale.

Categorization is thought to arise from partitioning of this underlying scale by five thresholds ($\theta_1, \theta_2 \ldots \theta_5$) which are assumed to be the same for all cultivars. A plant is assigned to category 1 of the ordinal scale if the value of y is less than or equal to the threshold θ_1. A plant is assigned to category 2 if its value of y lies between θ_1 and θ_2, and so on. Finally, the plant is assigned to category 6 if its value of y is larger than the threshold $\theta 5$. To estimate parameters two restrictions must be made. First, the origin of the underlying scale has to be fixed, which is done by taking $\theta_1 = 0$. Second, the scale parameter has to be fixed, which is done by taking $\sigma_B^2 = 1$. As a consequence, the probabilities that a plant of cultivar j in block i is assigned to categories 1, 2...6, respectively are given by

$$p_{ij}^1 = \Phi(-[\mu + \beta_i + \gamma_j + e_{ij}])$$
$$p_{ij}^c = \Phi(\theta_c - [\mu + \beta_i + \gamma_j + e_{ij}]) - \Phi(\Theta_{c-1} - [\mu + \beta_i + \gamma_j + e_{ij}]) \quad c = 2...5; \theta_1 = 0$$
$$p_{ij}^6 = 1 - \Phi.(\theta_5 - [\mu + \beta_i + \gamma_j + e_{ij}])$$

where Φ denotes the probability distribution function of the standard normal distribution. The probabilities p_{ij}^c may be considered as areas under a normal probability density function with mean $y_{ij} = \mu + \beta_i + \gamma_j + e_{ij}$ and unit variance. A graphical representation of the model is given in Figure 1.

Estimates of all unknown parameters (μ, β_i, β_j, θ_c, and σ_P) can be obtained simultaneously by maximum likelihood with the computer package Genstat (18). Furthermore, deviance statistics (16) are calculated, which are similar to sum-of-squares used in ANOVA. Values of a deviance statistic have to be compared with the table of the chi-squared distribution with the appropriate number of degrees of freedom. (A Genstat procedure as well as a Fortran program can be obtained for a nominal fee from the second author.)

Analysis of weight changes. The relative weight change (RWC) per block of a cultivar was calculated as the ratio of the weight change (final weight minus initial weight) of the four plants cultivated in infested soil and the weight change of the four control plants. Values of RWC were analyzed by ANOVA.

Correlations. Correlation diagrams were made to investigate the relation between DSS data and RWC data. To investigate reproducibility, correlations between the two independent experiments were calculated for both DSS and RWC data.

Combining categories of the ordinal scale. The disease rating data were regrouped into three new categories (i.e., old category 1+2, 3+4, and 5+6) or two new categories (i.e., old category 1+2+3 and 4+5+6) to determine whether or not a disease rating with fewer than six categories would lead to less discriminating power relative to a rating with six categories.

Classification of cultivars. Cultivars were classified with regard to resistance so that most of the variation among cultivars could be attributed to variation among groups rather than to variation

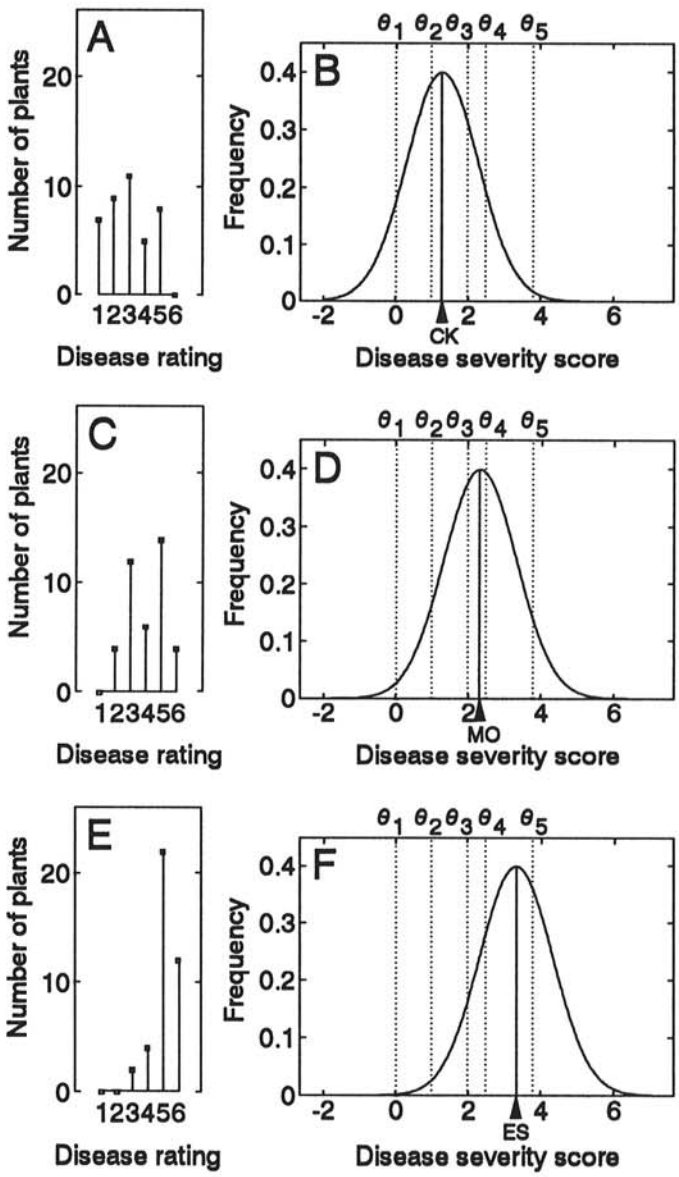

Fig. 1. Representation of ordinal disease rating data for three lily cultivars infected by *Fusarium oxysporum* f. sp. *lilii*. Data were analyzed according to a threshold model for ordered categorical data. **A, C, E,** Distribution of disease ratings for resistance for Connecticut King (CK), Montreux (MO), and Esther (ES), respectively. **B, D, F,** Corresponding normal distributions and disease severity scores according to the threshold model with five thresholds ($\theta 1 \ldots \theta 5$).

within groups. The criterion for classification was the deviance for differences between cultivars within groups. This deviance reached a maximum when all the cultivars were classified in a single group and a minimum (zero) when the number of groups was equal to the number of cultivars. To obtain a concise representation of the results, the number of groups must be as small as possible. Results can be represented in a dendrogram similar to that proposed by Caliński and Corsten (6) for continuous data.

RESULTS

Bulbs used in the 1990 experiment were cultivated under standardized conditions and without fungicides, so results of this experiment are assumed to be more reliable than those from 1989 and are emphasized here.

Results of the 16 cultivars with regard to disease rating with six categories, estimated DSS values, and corresponding standard error of differences (relative to Connecticut King) of the 1990 experiment are given in Table 1. The deviance for differences between cultivars is equal to 221.2 based on 15 degrees of freedom, which shows that large differences in resistance to *Fusarium* exist between the different cultivars ($P < 0.001$). Significant block effects did not occur (deviance equal to 4.7 with 9 degrees of freedom). The estimate of the between-pot variance (σ_P^2) is 0.17 (SE = 0.124). Estimates and SE of the thresholds are 0 (fixed), 0.98 (SE = 0.117), 1.95 (SE = 0.132), 2.47 (SE = 0.139), and 3.76 (SE = 0.165).

The weight data (average initial and average final weight) per cultivar per treatment in the 1990 experiment are given in Table 2. The initial weight of bulblets within cultivars was similar. Among cultivars, the average initial weight per bulblet ranged from 0.27 (Pirate) to 0.89 g (Esther) with an overall average of 0.55 g. In the control, the absolute increase of weight ranged from 0.34 (Pirate) to 5.77 g (Mont Blanc). Variation in resistance level, calculated as RWC among cultivars was observed (Table 2). The analysis of variance indicated highly significant differences among cultivars ($P < 0.001$) with no block effects detected.

TABLE 1. Number of bulblets in six disease categories and disease severity score (DSS) obtained by the threshold model, after planting scale bulblets of 16 Asiatic lily cultivars in *Fusarium*-infested soil (1990 experiment)

Cultivar	Disease category						DDS	
	1	2	3	4	5	6	Estimate	SED[a]
Connecticut King (CK)	7	9	11	5	8	0	1.29	...
Mont Blanc (MB)	0	12	15	8	5	0	1.52	0.245
Prominence (PR)	1	8	17	9	3	2	1.65	0.245
Orlito (OR)	2	6	16	8	6	2	1.75	0.245
Napoli (NA)	0	5	19	9	7	0	1.79	0.245
Hilde (HI)	1	4	11	11	11	2	2.10	0.247
Milano (MI)	0	4	13	5	17	1	2.21	0.247
Montreux (MO)	0	4	12	6	14	4	2.33	0.248
Yellow Blaze (YB)	1	6	8	7	11	7	2.35	0.249
Golden Melody (GM)	2	2	8	5	20	3	2.43	0.249
Sterling Star (ST)	0	3	4	8	20	5	2.72	0.252
Snow Star (SN)	1	1	8	7	11	12	2.85	0.254
Enchantment (EN)	0	0	0	3	29	8	3.33	0.261
Esther (ES)	0	0	2	4	22	12	3.37	0.261
Aristo (AR)	0	0	1	1	8	30	4.39	0.293
Pirate (PI)	0	0	1	0	3	36	4.99	0.338

[a] Standard error of differences, and refer to differences with Connecticut King.

TABLE 2. Initial weight, final weight, and relative weight change (RWC) of scale bulblets of 16 Asiatic lily cultivars planted in control and *Fusarium*-infested soil (1990 experiment)

Cultivar	Initial weight (g)[a]		Final weight (g)[a]		RWC[b]
	Control	Infested	Control	Infested	
Connecticut King (CK)	0.45	0.44	5.78	1.96	0.34
Napoli (NA)	0.54	0.57	5.12	1.65	0.24
Milano (MI)	0.56	0.54	6.24	1.65	0.24
Prominence (PR)	0.52	0.54	5.45	1.49	0.21
Mont Blanc (MB)	0.58	0.56	6.35	1.62	0.20
Orlito (OR)	0.54	0.52	5.09	1.13	0.14
Golden Melody (GM)	0.61	0.56	4.79	1.15	0.14
Hilde (HI)	0.67	0.56	5.40	1.08	0.12
Montreux (MO)	0.56	0.46	5.97	0.93	0.09
Enchantment (EN)	0.36	0.37	5.10	0.68	0.07
Sterling Star (ST)	0.57	0.62	5.46	0.93	0.07
Yellow Blaze (YB)	0.70	0.72	4.72	0.86	0.04
Snow Sar (SN)	0.59	0.59	4.60	0.65	0.02
Esther (ES)	0.89	0.76	4.06	0.53	−0.08
Aristo (AR)	0.59	0.59	2.27	0.13	−0.36
Pirate (PI)	0.27	0.28	0.62	0.01	−0.69
SED[c]					0.072

[a] Each value is the mean of 40 plants.
[b] Each value is the mean of 10 blocks.
[c] Standard error of differences.

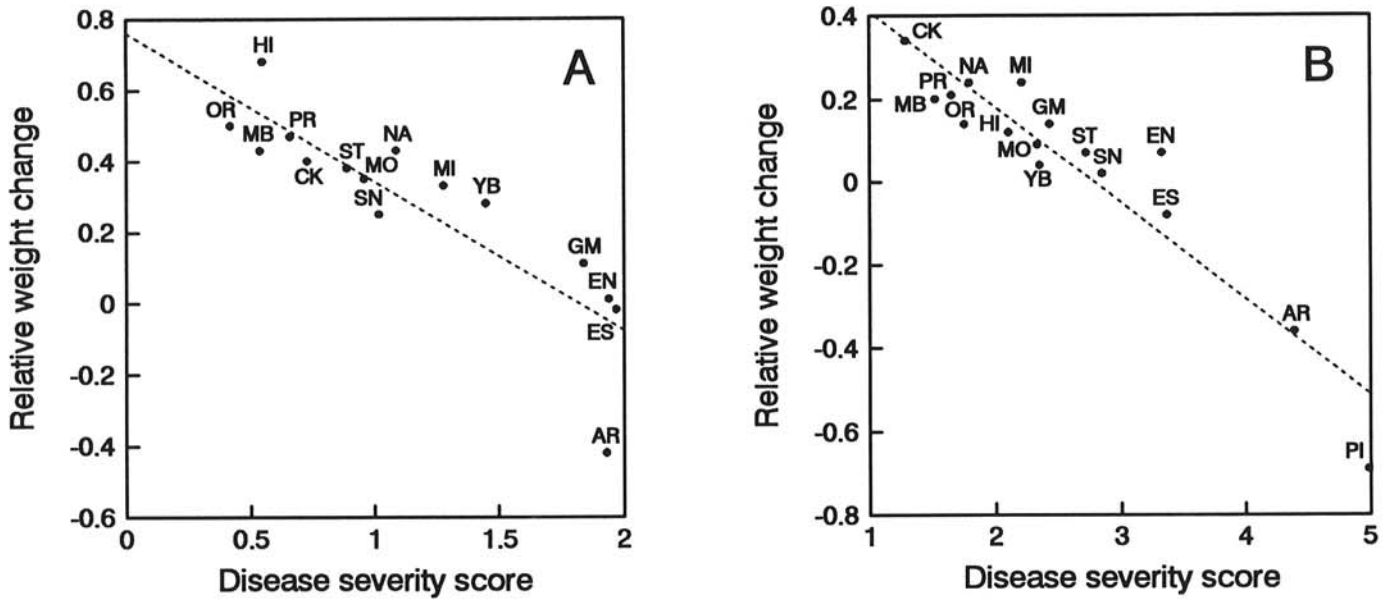

Fig. 2. Correlation diagram between disease severity score obtained by the threshold model with six categories and the relative weight change of scale bulblets of 16 Asiatic lily cultivars planted in *Fusarium*-infested soil. See Table 1 for abbreviations of cultivars. A, 1989 ($r^2 = 0.75$). B, 1990 ($r^2 = 0.88$).

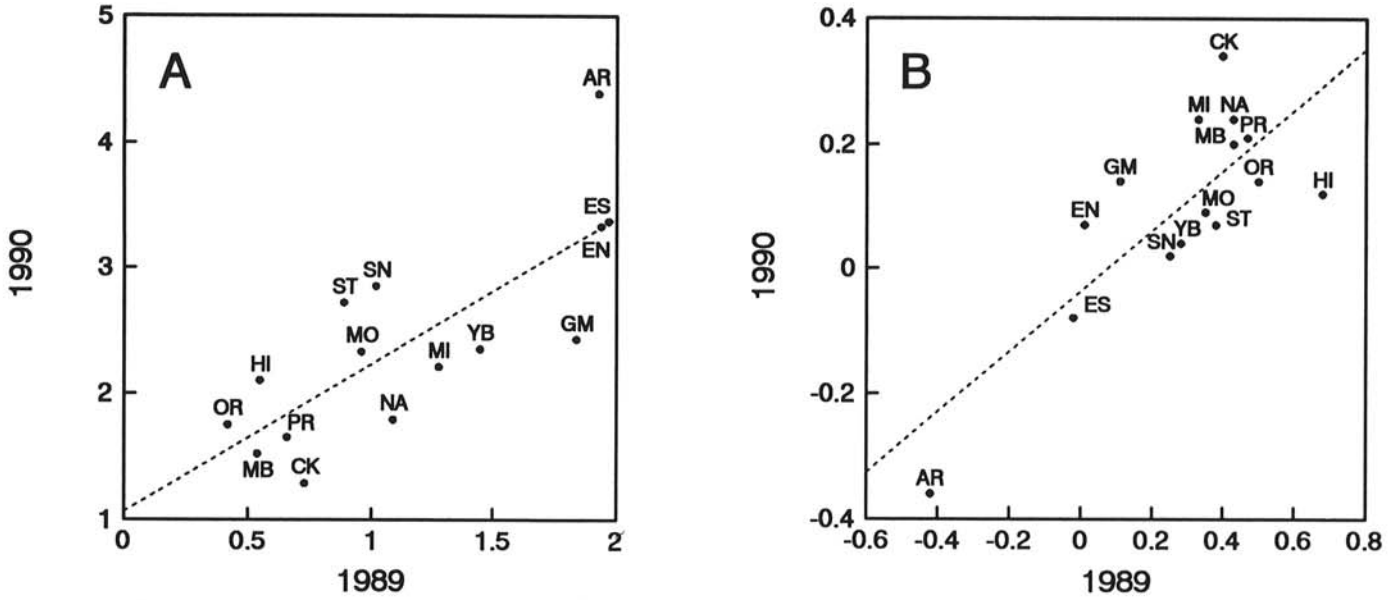

Fig. 3. Correlation diagram between results of the 1989 and 1990 experiments with scale bulblets of 15 Asiatic lily cultivars planted in *Fusarium*-infested soil. See Table 1 for abbreviations of cultivars. **A,** Disease severity scores obtained by the threshold model with six categories ($r^2 = 0.61$). **B,** Relative weight change ($r^2 = 0.62$).

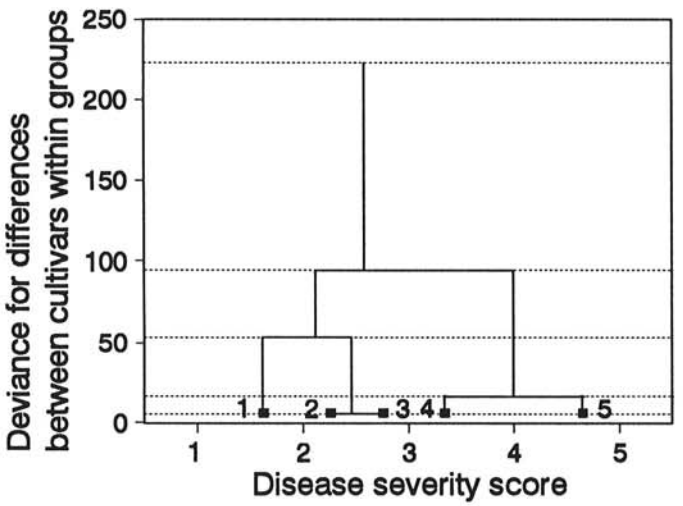

Fig. 4. Deviances for differences between cultivars within groups and corresponding disease severity scores obtained by the threshold model with six disease categories, after classification of cultivars in different groups (1990 experiment). Group 1 = CK, MB, PR, OR, NA; group 2 = HI, MI, MO, YB, GM; group 3 = ST, SN; group 4 = EN, ES and group 5 = AR, PI. See Table 1 for abbreviations of cultivars.

To investigate the relationship between the RWC data and the DSS data, correlation diagrams were made (Fig. 2). A high correlation between DSS, obtained from the threshold model with six categories, and RWC was observed. Correlations between the 1989 and 1990 experiments for both DSS and RWC data are presented in Figure 3. Results of both years were correlated for DSS as well as RWC.

Analysis of regrouped data in two or three categories still gave highly significant differences between cultivars ($P < 0.001$). The deviance, however, was smaller (189.1 for three categories and 148.4 for two categories) than the deviance obtained with six categories (deviance = 221.2). This indicates that discrimination was reduced by combining categories.

A dendrogram (Fig. 4) based on disease ratings in six categories indicates that a division of the 16 cultivars into two groups led to a deviance of 94.1 (with 14 degrees of freedom) for differences between cultivars within groups. Further division into three, four, or five groups led to deviances of 53.0 (with 13 degrees of freedom), 17.0 (with 12 degrees of freedom), and 6.2 (with 11 degrees of freedom), respectively. A classification with four groups provided an adequate summary of the variation among cultivars, yet kept the number of groups acceptably small. Such a classification accounted for 92% of the differences among cultivars. Borders between groups were found where large intervals of DSS existed between cultivars, i.e., Napoli and Hilde, Snow Star and Enchantment, and Esther and Aristo (Table 1).

DISCUSSION

Disease severity in lily scale bulblets was measured and analyzed in two different ways. In the first analysis, disease rating data were used, in which plants were assigned to the categories of an ordinal scale according to the severity of symptoms. This method of evaluating disease severity is relatively easy and, therefore, commonly used. Analysis of these data is difficult, however. The threshold model for analyzing ordered categorical data is a fairly new approach that involves an underlying linear scale (9,10,15).

Categories of the disease rating scale must be well-defined to obtain consistent results. A large number of categories improves discrimination between disease severity levels but increases the difficulty of assigning plants to specific categories. Moreover, the chance of rating errors or empty categories increases. On the DSS scale, thresholds mark the borders of the disease rating categories. The distance between thresholds determines how precisely categories are chosen. In this study, six categories were used, and fewer plants were assigned to category 4 than to either categories 3 or 5. This conforms with the relatively small estimated difference between thresholds 3 and 4 and may be due to the fact that symptom development in the bulbs progresses at a variable rate after infection.

Adjacent categories were combined to study the effect of using a reduced number of categories. When two or three categories were used instead of six, however, deviances were reduced and led to less discrimination between the cultivars. When only two categories were used, the model was reduced to a binomial model in which plants were classified as only healthy or diseased. The reduction of the deviance with two categories is due to the fact that a part of the information is discarded, i.e., severity of symptoms is not considered.

Although almost all scale bulblets were infected in the experiments, large cultivar effects occurred. The cultivars Aristo

and Pirate both had a rather high standard error of differences compared to the other cultivars, which means that the DSS estimates of Aristo and Pirate is less reliable than the DSS estimates of the other cultivars. This occurred because both Aristo and Pirate were severely diseased and received disease ratings mainly in the high categories.

Disease ratings, although rated on a progressively coarser scale with a limited number of categories, are often analyzed by analysis of variance. An analysis of variance on the disease rating data presented in this paper provided results similar to those obtained with the threshold model (not shown). Standard errors of differences between cultivars as provided by analysis of variance were relatively underestimated compared to those obtained by the threshold model, however, especially if extremely susceptible or resistant cultivars were involved. The threshold model acknowledges the fact that discrimination becomes more difficult if cultivars are extremely resistant or extremely susceptible. In complex experiments involving several factors, analysis of variance may lead to inclusion of interactions that are caused by the limitations of the ordinal scale rather than the biology of the system.

Another way of estimating the disease severity was by calculation of the relative weight change of lily scale bulblets. Normally, bulblets gain weight during cultivation by developing shoots and by growing of the bulbs. Infection causes bulb rot, wilting, and stunting, and all are reflected in diminished weight increase or even weight decrease. Therefore, weight change of infected bulbs relative to weight change of control bulbs can express disease severity. Differences in RWC reflect the difference in disease severity of the cultivars used. As with DSS estimates, RWC data analyzed by analysis of variance revealed a large cultivar effect.

The RWC values apparently were not influenced by the initial weight of the bulblets because RWC values and initial weight were not correlated. Results might be influenced, however, by the vigor of the cultivars. The two most slowly growing cultivars also had the lowest RWC. Whether this slow growth biases the test results or low vigor implicates a high *Fusarium* disease severity is unclear.

The 1989 and 1990 experiments gave reproducible results for both DSS and RWC. Differences between the data sets might be due to differences in the origin of the bulbs.

Both methods described to estimate disease severity (DSS and RWC) gave clear results. The high correlation between results from those two methods in both years means that both methods adequately describe the same phenomenon, i.e., disease severity. In this case, however, both resistance and tolerance of cultivars must be considered. Both methods are based on symptoms, so neither method can discriminate between tolerance and resistance. Histological research indicated that genotypes with a low level of disease retard colonization (R. P. Baayen, *personal communication*), which suggests that resistance rather than tolerance is involved.

We expected that the weight measurements would reflect disease severity more precisely than the visible symptom scale because weight measurements are more objective than the disease ratings. The high correlation between RWC and DSS, however, indicates that the disease rating, if analyzed properly, can be used. Both methods provided similar precision. The weight measurement is labor intensive and needs a large experimental design (equal number of infested and control pots), which are important practical considerations. If disease ratings are used, only a small number of control plants have to be analyzed to determine whether or not bulbs were infected prior to the experiment. Although weight measurements can be analyzed easily compared with disease ratings, labor and greenhouse capacity involved in obtaining these measurements make their application in large screening tests impractical.

As expected from the choice of cultivars for this study, variation in resistance to *F. o. lilii*, although partial, was found in Asiatic cultivars of *Lilium*. Classification of cultivars into phenotypic groups would provide an adequate representation of the results of a screening test. In this study, at least four groups of cultivars, differing in resistance, could be distinguished by the disease rating analysis with six categories. Cultivars within groups can be treated as equivalents. Results can be used for purposes of practical breeding and variety research.

Whether the resistance level observed for some cultivars in this study is sufficient to justify reduced use of fungicides in commercial bulb cultivation is not yet clear. Cultivars that were resistant in this test (e.g., Connecticut King and Mont Blanc) did not exhibit disease symptoms when cultivated in the field. Cultivars that were susceptible in this test (e.g., Pirate and Esther) often have been susceptible under field conditions. Our results were also comparable with other reports (12,20).

The *Fusarium* test under standardized conditions combined with disease ratings, analyzed using the threshold model as applied in this study proved to be very suitable for detecting differences in resistance level among cultivars. Disease ratings provided reproducible results and a practical experimental design. This test will be used to compare *Fusarium* resistance of different developmental stages of lily bulbs in further research.

LITERATURE CITED

1. Bald, J. G., and Chandler, P. A. 1957. Reduction of the root rot complex on croft lilies by fungicidal treatment and propagation from bulb scales. Phytopathology 47:285-291.
2. Bald, J. G., Paulus, A. O., and Lenz, J. V. 1983. Control of field root and bulb diseases of Easter lily. Plant Dis. 67:1167-1172.
3. Bald, J. G., Suzuki, T., and Doyle, A. 1971. Pathogenicity of *Fusarium oxysporum* to Easter lily, narcissus and gladiolus. Ann. Appl. Biol. 67:331-342.
4. Bollen, G. J. 1972. Pathogenicity of fungi isolated from stems and bulbs of lilies and their sensitivity to benomyl. Neth. J. Plant Pathol. 83:317-329.
5. Boontjes, J. 1974. Chemical control of diseases in lilies. Acta Hortic. 47:137-142.
6. Caliński, T., and Corsten, L. C. A. 1985. Clustering means in ANOVA by simultaneous testing. Biometrics 41:39-48.
7. Duineveld, Th. L. J., and Beijersbergen, J. C. M. 1975. On the resistance to benomyl of fungi isolated from bulbs and corms. Acta Hortic. 47:143-148.
8. Imle, E. P. 1942. Bulbrot disease of lilies. The Lily Yearbook of the North Am. Lily Soc. 1942:30-41.
9. Jansen, J. 1990. On the statistical analysis of ordinal data when extravariation is present. Appl. Statist. 39:75-84.
10. Jansen, J. 1991. Fitting regression models to ordinal data. Biom. J. 33:807-815.
11. Komada, H. 1975. Development of a selective medium for quantitative isolation of *Fusarium oxysporum* from natural soils. Rev. Plant Prot. Res. 8:114-125.
12. Löffler, H. J. M., and Mouris, J. R. 1989. Screening for *Fusarium*-resistance in lily. Med. Fac. Landbouww. Rijksuniv. Gent 54/2b:525-530.
13. Löffler, H. J. M., and Rumine, P. 1991. Virulence and vegetative compatibility of Dutch and Italian isolates of *Fusarium oxysporum* f. sp. *lilii*. J. Phytopathol. 132:12-20.
14. Maginnes, E. A., and Smith, J. D. 1971. Scale test to assess susceptibility of lilies to various bulb rot organisms. The Lily Yearbook of the North Am. Lily Soc. 24:20-28.
15. McCullagh, P. 1980. Regression models for ordinal data (with discussion). J. R. Statist. Soc. B 42:109-142.
16. McCullagh, P., and Nelder, J. A. 1989. Generalized Linear Models. 2nd ed. Chapman and Hall, London.
17. McRae, E. A. 1987. Lily Disease Handbook. North Am. Lily Soc. 28 pp.
18. Payne, R. W., Lane, P. W., Ainsley, A. E., Bicknell, K. E., Digby, P. G. N., Harding, S. A., Leech, P. K., Simpson, H. R., Todd, A. D., Verrier, P. J., White, R. P., Gower, J. C., Tunnicliffe Wilson, G., and Paterson, L. J. 1987. Genstat 5, Reference Manual. Clarendon Press, Oxford.
19. Smith, J. D., and Maginnes, E. A. 1969. Scale test of hardy hybrid lilies. Can. Plant Dis. Surv. 49:43-45.
20. Van Tuyl, J. M. 1980. Lily breeding research of IVT in Wageningen. The Lily Yearbook of the North Am. Lily Soc. 33:75-82.
21. Van Tuyl, J. M. 1983. Effect of temperature treatments on the scale propagation of *Lilium longiflorum* 'White Europe' and *Lilium* × 'Enchantment'. HortScience 18:754-756.