Genetic Control of O₃ Sensitivity in a Cross Between Two Cultivars of Snap Bean

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ABSTRACT. Identification of genetic control of ozone (O₃) sensitivity is desirable for selection of plant cultivars which are indicators of O₃ stress. A cross was made between two cultivars of snap bean (Phaseolus vulgaris L.), ‘Oregon 91’ (P₁) and ‘Wade Bush’ (P₂), an O₃-sensitive and O₃-insensitive cultivar, respectively. Ten genetic populations (generations), ‘Oregon 91’ (P₁), ‘Wade Bush’ (P₂), F₁, F₂, backcrosses to both parents, and all reciprocal crosses, were field planted in each of two summers and evaluated for injury to O₃. Ozone responses for the reciprocal crosses were not significantly different for any generation, so injury ratings from the reciprocal crosses were combined for each generation to provide six populations (P₁, P₂, F₁, F₂, BC₁, and BC₂) for analysis. When components of genetic variation were estimated from the six generations, additive genetic variance was the most important component in the total genetic variance available, although dominance variance was also a significant component. There was an inconsistency in the magnitude and the direction of the factors contributing to the dominance effects and also a large environmental component making up the phenotypic variance. Estimates of broad-sense heritability and narrow-sense heritability were 60% and 44%, respectively. Results suggest that O₃-sensitive and O₃-insensitive selections could be screened and evaluated in an ambient O₃ environment. Several generations will be necessary, however, to develop Bush Blue Lake type selections that vary only in sensitivity to O₃.

Materials and Methods

The bean genotypes chosen as parents were ‘Oregon 91’ (P₁), (O₃ sensitive), a white-seeded BBL cultivar and ‘Wade Bush’ (P₂), (O₃ insensitive), a dark-seeded bush snap bean. Both cultivars have stable responses to ambient O₃ in the field. Parents were crossed in a charcoal-filtered glasshouse during 1991 and 1992 to obtain an F₁ population. A portion of seed from the F₁ population was sown in the glasshouse to obtain the F₂ population. Another portion of the F₂ population was backcrossed to both parents. Hypocotyl and flower colors served as markers to confirm successful hybridization and all crosses were made reciprocally. This gave 10 genetic populations (generations): the two parents (‘Oregon 91’ and ‘Wade Bush’), the F₁ (‘Oregon 91’ x ‘Wade Bush’), the F₂ (‘Oregon 91’ x ‘Wade Bush’), the F₃ (selfs from both F₁ populations), and the backcrosses (P₁ x F₁, F₁ x P₂, P₂ x F₁, F₁ x P₂).

The 10 populations were hand planted in the field at the Central Crops Experiment Station, Clayton, N.C., during Summers 1992 and 1993. The field design for each year consisted of four replications of 10-plant plots. To avoid low plant numbers from poor germination or poor seedling growth, nonsegregating generations in each replication were double-seeded and thinned to the 10 plants exhibiting the best growth habit 20 d after seeding. Segregating generations, the F₃, and backcross generations, were expected to have the greatest amount of variation in sensitivity to...
O₃. These generations were not double seeded, but were planted in four, 10-plant plots per replication to provide a larger number of individual plants for evaluation. Cultural errors and soilborne disease resulted in fewer than 10 plants per row and even the loss of several whole plots by the end of the growing season.

Standard bean cultural practices for the North Carolina piedmont were followed, but timing of cultural practices varied slightly between years depending on weather conditions suitable for providing the necessary fertilization and insect control. Two insecticides, Asana (esfenvalerate)(DuPont Agricultural Products, Wilmington, Del.) and Talstar (biphenthrin) (FMC Corp., Philadelphia, Pa.), were used as needed in this study, because they did not have any phytotoxic effects on bean and provided adequate control of insects of concern, including white fly (Aleyrodidae sp.), spider mite (Tetranychus urticae) and Western flower thrips (Frankliniella occidentalis). Plants were irrigated as needed to keep field moisture conditions high.

Hypocotyl color of each plant was recorded in the seedling stage, and as the plant matured, flower color was determined. Data from these markers were used to check segregation ratios for the crosses. Individual plant O₃-injury ratings were made 42 and 52 d after seeding representing the full-flowering and the pod-fill stages of plant growth. Because of the large number of plants, individual leaves were not rated. Injuries of the total leaf surface were evaluated on a 0 to 10 scale. A rating of zero (0) was given if there was no injury, and a rating of 10 was assigned when all leaves were injured and/or abscised.

Injury ratings were analyzed using a least squares analysis weighted by the inverse of the number of plots (observations) per generation mean (Halward and Wynne, 1991). Mean squares were examined to determine whether or not generations differed for severity of O₃ injury and whether or not these differences were consistent over the 2 years. Reciprocal crosses were tested for homogeneity of response using contrast statements. Since they did not have any phytotoxic effects on bean and provided adequate control of insects of concern, including white fly (Aleyrodidae sp.), spider mite (Tetranychus urticae) and Western flower thrips (Frankliniella occidentalis). Plants were irrigated as needed to keep field moisture conditions high.

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Rowe and Alexander (1980) modified the methods of Mather and Jinks (1977) to better estimate the standard errors of the parameter estimates, and their matrix notation was followed for this analysis. The following matrices were used in the generation means analysis: a) the diagonal matrix of the number of plots per generation, b) the diagonal matrix of the variances of the six generations, c) the vector of generation least square means, and d) the matrix of the genetic expectations of the generation means in terms of the three parameters from the additive-dominance model. These matrices were used to solve for the estimates and standard errors of the additive-dominance model parameters: m, d, and h, where m represents the midparent value, d represents the sum of the differences between the homozygote and the midparent (additive effect), and h represents the sum of the differences between the heterozygote and the midparent (dominance effect), respectively (Mather and Jinks, 1977). The expected means for the generations were generated as the product of the matrix of expectations and the matrix of estimates of the model parameters. The squared deviations between the observed and expected generation means were summed to obtain an chi-square value with three degrees of freedom and used to test the adequacy of the model.

Separate analyses were run for each generation with data from all replications and both years. Components of genetic variation were estimated from the six generations available using the plant to plant variances from the one-way analysis of variance and the following formulas from Mather and Jinks (1977):

\[ E = \sigma_p^2 + \sigma_h^2 - 2(\sigma_{F1}^2 + \sigma_{BC1}^2) \]

\[ D = 4\sigma_p^2 - 2(\sigma_{BC1}^2 + \sigma_{BC2}^2) \]

\[ H = 4(\sigma_{BC1}^2 + \sigma_{BC2}^2) - \sigma_{F1}^2 - \sigma_{F2}^2 - \sigma_{BC}^2 \]

\[ F = \sigma_{BC1}^2 - \sigma_{BC2}^2 \]

Where P₁ is ‘Oregon 91’ and P₂ is ‘Wade Bush’ and BC₁ and BC₂ are the backcrosses to these parents respectively. From these variance components, the dominance ratio and consistency of sign and magnitude of effects were determined.

### Results

Significant differences were detected among generation mean squares for each injury evaluation. Following the first injury reading, there was a significant difference between years, among replications, and among generations. The year × generation interaction was not significant (Table 1). Following the second injury reading, there were only differences between replication and among the different generations. There were no significant differences between years or interaction between years and generations (Table 1). The mean values for each generation (Table 1) showed that with both injury scores, ‘Oregon 91’ (P₁) had significantly more injury than ‘Wade Bush’ (P₂). The average injury score of F₁ plants from both injury evaluations did not differ from P₁, but differed from P₂. The F₂ generation had an average mean score following the first reading that was not different from P₁, but was different from P₂. However, following the second injury evaluation period, the average injury value of

| Source      | df | Injury 1       | Injury 2       |
|-------------|----|----------------|----------------|
| Year        | 1  | 2.414**        | 0.331          |
| Rep (year)  | 6  | 2.916*         | 23.772**       |
| Generation  | 5  | 4.677**        | 32.103**       |
| Year × generation | 5 | 0.347          | 0.749          |
| Error       | 29 | 0.197          | 0.206          |

| Generation | Mean injury score 1 | Mean injury score 2 |
|------------|---------------------|---------------------|
| Parent (P₁) Oregon 91 | 1.76 ab² | 4.50 a |
| Parent (P₂) Wade Bush | 0.95 c | 2.05 d |
| F₁         | 2.07 a            | 4.76 a            |
| F₂         | 1.75 ab           | 3.93 b            |
| P₁ x F₁    | 2.19 a            | 4.83 a            |
| P₂ x F₁    | 1.52 b            | 3.49 c            |

²Mean separation within columns by Waller-Duncan K ratio (K = 100) t test.

* **Significant at $P = 0.05$ or 0.01, respectively.
the F2 generation was different from both P1 and P2. The backcross of the F1 x P1 generation was not different from P1, but was different from P2, following both injury evaluations. This meant the F1 backcross to the O3-sensitive parent was as sensitive as the sensitive parent.

Generation means and variances from the second O3 injury ratings from the ‘Oregon 91’ x ‘Wade Bush’ cross were used for further analysis (Table 2). The number of observations (n) is based on number of plots (10 plants per plot). The experiment was designed to allow greater n values for those populations expected to have greater variation due to plant segregation (F1 and backcross generations). The variance for each generation is given and weighted for each generation by the n value. The estimates presented in Table 3 were used to calculate the expected injury means for each generation given in Table 2. The chi-square value given in Table 3 was not significant and thus, the additive dominance model was adequate for our data without additional terms to account for interactions between genes at different loci.

The variances within snap bean generations for O3 injury are presented for each family in Table 4. The genetic expectations for these variances are also listed for each generation, along with the components, estimates, and a description of each component. These data show there is a higher level of additive than dominance genetic variance and a sizeable environmental variance component. Most of the environmental variance can be explained by the phenotypic variation of growth and development in the presence of changing environmental factors. These are probably factors affecting the general sensitivity to O3 rather than year to year changes, because variance estimates were based on plant to plant variation.

The distribution or percentage of total plant numbers at each score level within each generation are presented in Figs. 1 to 3. In the case of ‘Oregon 91’ (Fig. 1A), 62.3% of the plants scored 5 or above. The backcross of the F1 to ‘Oregon 91’ was more like ‘Oregon 91’, since 58.4% of the plants scored a 5 or above (Fig. 3A). In the case of ‘Wade Bush’, 97.3% of the plants scored a 5 or below. The backcross of the F1 to ‘Wade Bush’ was more like ‘Wade Bush’, since 83.6% of the plants scored a 5 or below (Fig. 3B). In the F1 (Fig. 2A), 55.5% of the plants scored a 5 or above, which was nearly identical to ‘Oregon 91’ (62.3%), and with the F1 population (Fig. 2B) this value was 40.8%. The percentage of plants scoring injury of 4 to 6 in the F1 generation was 60% and segregation of sensitive and insensitive plants was rather evenly distributed.

### Table 2. Generation means and variances for O3-injury rating 2 from a cross between two snap bean cultivars, ‘Oregon 91’ and ‘Wade Bush.’

| Generation | n | \(V_x\) | \(W_t = 1/V_x\) | m | d | h | Observed | Expected | (Obs–Exp)* |
|------------|---|---------|-----------------|---|---|---|----------|----------|------------|
| P1 (Oregon 91) | 7 | 0.5659 | 1.7670 | 1 | 1 | 0 | 4.496 | 4.685 | -0.1898 |
| P2 (Wade Bush) | 8 | 0.5659 | 1.7670 | 1 | -1 | 0 | 2.049 | 2.045 | 0.0041 |
| F1 | 16 | 0.5669 | 1.7670 | 1 | 0 | 1 | 4.761 | 4.842 | -0.0810 |
| F2 | 68 | 0.7397 | 1.3519 | 1 | 0 | 0.5 | 3.928 | 4.104 | -0.1759 |
| P3 x F1 | 68 | 0.3406 | 2.9362 | 1 | 0.5 | 0.5 | 4.828 | 4.764 | 0.0640 |
| P2 x F1 | 64 | 0.3406 | 2.9362 | 1 | -0.5 | 0.5 | 3.486 | 3.443 | 0.0424 |

*The model lists the coefficients by generation for the genetic components in the additive-dominance model; m = the midparent; d = the additive component; h = the dominance component.

**Number of observations (10-plant plot rows) per generation over 2 years: 1 plot x 4 reps x 2 years for nonsegregating parental plots; 2 reciprocals x 1 plot x 4 reps x 2 years for nonsegregating F1 plots; 2 reciprocals x 4 plots x 4 reps x 2 years + 4 extra plots for segregating F2 and backcross plots.** One parental and four backcross F2 x F1 plots were lost.

**Variance of the mean; Wt is the reciprocal of the variances of the means, and the weighted values take into consideration the differing number of observations within each generation.**

**Obs – Exp = observed minus expected.**

### Discussion

The cross of ‘Oregon 91’ x ‘Wade Bush’ was chosen because both were determinate snap bean cultivars with differences in O3 sensitivity. The F1 generation was different from both P1 and P2. The backcross of the F1 x P1 generation was not different from P1, but was different from P2, following both injury evaluations. This meant the F1 backcross to the O3-sensitive parent was as sensitive as the sensitive parent.

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### Table 3. Estimates with standard errors based on the three-parameter genetic model for O3-injury rating 2 for the cross between ‘Oregon 91’ and ‘Wade Bush’ snap beans.

| Genetic parameter | Estimate | SE | \(P > t\) |
|------------------|----------|----|---------|
| m*               | 3.365    | 0.177 | 0.001  |
| d*               | 1.320    | 0.112 | 0.001  |
| h*               | 1.476    | 0.336 | 0.001  |

Chi-square value = \(\chi^2(3) = 4.641\); \(p = 0.25\).

*\(m =\) midparent or midpoint between the two homozygous parents.

**\(d =\) additive genetic component; d is the sum of the differences between the homozygotes and the midparents (over all factors involved in the expression of O3 sensitivity).

**\(h =\) dominance genetic component; h is the sum of the differences between the heterozygotes and the midparents (over all factors involved in the expression of O3 sensitivity).

**The chi-square value is the sum of the squared, weighted differences between the observed and expected means for the six generations. Since the probability of obtaining a greater chi-square is nonsignificant, the additive-dominance model is considered to adequately explain the data.**

### Table 4. Variances within snap bean generations for O3-injury rating 2 in the cross between ‘Oregon 91’ and ‘Wade Bush’ snap beans.

| Component | Estimates |
|-----------|-----------|
| D         | 3.343     |
| H         | 2.576     |
| F         | -0.710    |
| Ew        | 1.588     |
| (H/D)0.05 | 0.853     |
| F/(DxH)0.05 | -0.235  |

**Component:** Additive component, Dominance component, F = S\(sd\); negative denotes dominance of Wade (BC has smaller variance).

**Environmental variance, high level of dominance, inconsistency of hs in sign.**
sensitivity and with convenient markers (different hypocotyl and flower colors) for monitoring hybridization success. We have attempted to determine the heritability and genetic variance of O₃ sensitivity for that cross. The total genetic variance for this cross was determined and subdivided into the additive genetic variance and dominance genetic variance. The additive-dominance model was found adequate without additional terms for genetic interaction.

This additive-dominance model assumes that the mean of the phenotypes, in this case visual injury due to O₃, can be estimated by three parameters. These parameters are a midpoint value, m, an additive component, d, and a dominance component, h (Mather and Jinks, 1977). In this cross, these estimates were significantly different from zero, and the model adequately described the injury data for the generational means examined. Thus, no significant epistatic or gene interaction effects needed to be added to the model, and the additive and dominance genetic effects were well estimated. One of the limitations of the generation means analysis is that it is based on mean phenotypes, thus masking the individual effects of multiple genes if all genes do not contribute in the same direction and magnitude to the character of interest (Mather and Jinks, 1977).

When individual plant data are available, variances within the generations can be used to estimate the additive (D), dominance (H), crossproducts (F), and environmental (E) components of the genetic variation available from the cross between two cultivars. Because of the nature of second order statistics, interpretation of estimated effects is not limited by any lack of consistency in sign and magnitude as is experienced with first order statistics (Mather and Jinks, 1977). The variance components refined the information in the generation means analysis. The dominance ratio confirmed the importance of dominance in the model, whereas, the ratio of F/(D×H)(0.05) indicated inconsistencies in sign and magnitude of the dominance deviations at the different loci.

Mebrahtu et al. (1990) performed a generation means analysis and found the additive-dominance model adequate, but their crosses...
involved BBL O₃-sensitive cultivars with two O₃-resistant dry bean plant introductions. They found some dominance toward insensitivity to O₃ and mostly additive genetic variance. Inconsistencies between their results and ours are most likely due to the very different numbers of plants in each population. Whereas, both research efforts included sensitive, white-seeded BBL cultivars, we used a dark-seeded determinate snapbean as an O₃-insensitive parent and Mebrahtu et al. (1990) used dark-seeded indeterminate dry bean plant introduction acquisitions. Other research with dry beans has also indicated dominance toward insensitivity (Guri, 1983; Hucl and Beversdorf, 1982b). Dry beans are indeterminate and slower to mature than snap beans and maturity can confound the O₃ sensitivity ratings (Hucl and Beversdorf, 1982a). On the other hand, Butler et al. (1979) found dominance towards sensitivity to O₃ and their work also involved dry bean cultivars. Most of these studies had inadequate plant numbers due to constraints of exposure systems used in the research.

Our broad-sense heritability estimate was 60.3% and the narrow-sense estimate was 44.2% for visible injury. Broad-sense heritability refers to the proportion of the total variability that is due to genetic causes, or the ratio of the genetic variance to the total variance. If broad-sense heritabilities are small, the distinction of genotype based on phenotypic differences is less clear. Since the total additive genetic variance in relation to phenotypic variance, as measured by narrow-sense heritability was moderate, selection of genotypes for high O₃ sensitivity and low O₃ sensitivity will require some time. Mebrahtu et al. (1990) did not give any heritability estimates in their study, and although the broad-sense heritability in the cross between ‘Blue Lake Stringless’ x ‘Black Turtle Soup’ (Butler et al., 1979) was high (83%), the O₃ exposure concentration was also high (1300 µL-L⁻¹). The plant numbers used in the latter study were extremely low and may not have adequately represented the generations of plants involved. Broad-sense heritability estimates were also high (66% to 88%) in the F₁ generation from bean crosses made by Hucl and Beversdorf (1982b). In the F₁ generation broad-sense heritability estimates were low (16% to 21%). It is difficult to compare results of these crosses with our study because of different plant populations and O₃ exposure regimes.

Heritabilities in our study suggest that perhaps large environmental effects existed. The large environmental component in our study was probably due to all the factors that affect bean sensitivity to O₃, including temperature, humidity, light, soil nutrition, insects, and diseases, and perhaps most importantly, changes in stomate function and uptake of O₃. Stomate function has been studied using genotypes with varying sensitivities of bean and petunia (Butler et al., 1979; Hucl and Beversdorf, 1982a; Thorne and Hanson, 1976). Engle and Gableman (1966) found that resistance to O₃ was controlled by a single dominant gene thought to be responsible for loss of guard cell permeability. Guard cells of an O₃-resistant onion were sensitive to O₃ and lost their permeability, allowing stomatal closure, while in the susceptible plant, the guard cells were not as sensitive to O₃ and allowed O₃ to pass into the substomatal cavity.

In the present study, one of the reasons for understanding the inheritance patterns for the cross between ‘Oregon 91’ x ‘Wade Bush’ was to determine possibilities for identifying highly O₃-sensitive and O₃-insensitive selections which are as phenotypically similar as possible. Our data indicated that because of the significant dominance component, selection for extremes in O₃ sensitivity should follow several generations of selfing. These selections could be used in developing lines highly suitable for determining physiological and biochemical mechanisms related to variation in sensitivity to O₃ in snap bean. In addition, O₃-sensitive and O₃-insensitive selections, if similar in yield under O₃-free environments, would be expected to produce different yields related to their O₃ sensitivity in ambient O₃ environments. These selections could be used as seed sources of a plant indicator system in the same way as white clover (Trifolium repens) clones have been developed and used as a cloned O₃ indicator and/or monitoring system (Heagle et al., 1995).

Our research differed from other studies of the inheritance of sensitivity of Phaseolus vulgaris to O₃ reported in the literature. Previous studies (Butler et al., 1979; Guri, 1983; Hucl and Beversdorf, 1982b) have involved dry bean cultivars as both parents or at least one of the parents, but did not involve backcrosses of the F₁ to the parents. The study of Mebrahtu et al. (1990) involved backcrosses, but they did not examine variance components. The focus of our investigations was to develop a cross between an O₃-sensitive BBL snap bean with known pedigree and an O₃-insensitive determinate type bush snap bean with

![Injury rating scale (10 = 100% ozone-Injured)](image-url)

Fig. 3. Percentage of the total number of plants in each injury class; (A) F₁ x F₁ and (B) F₂ x F₂.
colored seed. We also included reciprocal crosses in our investigations. Another difference in this research from the other studies is that results of the study were based on field injury evaluations involving sufficiently high numbers and replications of individual plants to make adequate evaluations of each generation. In other studies (Butler et al., 1979; Guri, 1983) plant numbers were few and determination of inheritance was made on injury developed from experimental exposures to O₃ using varying kinds of exposure chambers.

In conclusion, it appeared possible from this study that O₃-sensitive and O₃-insensitive selections from this cross could be screened and evaluated in an ambient O₃ environment. Results of this study showed that dominance for sensitivity to O₃ was an important component in the total genetic variance available in the cross between 'Oregon 91' and 'Wade Bush' snap beans. Additive genetic variance, the useful component with a self-pollinated crop, was also a significant component of the genetic variation and a stronger contributor to the total genetic variance than dominance. This information coupled with a large environmental component making up the phenotypic variance, and an understanding of environmental impacts on O₃ response in bean, highlight the challenges in breeding snap bean with insensitivity to O₃. Several generations will be necessary to develop BBL-type selections which are similar and vary only in sensitivity to O₃. Results of such research could be valuable tools in understanding the still elusive mechanism by which O₃ damages crops.

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