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Title: The Genetic Analyses of Neck-rot (Botrytis allii) Resistance, Pungency and Soluble Solids Content of Onion (Allium cepa).

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The inheritance of resistance to neck-rot incited by Botrytis allii Munn, pyruvic acid content, and soluble solids content and the relationships of these characters in onion (Allium cepa L.) were studied. A total of 10 inbred onion lines were involved in a nine-parent diallel cross and six individual crosses for which parental, F_1, F_2, and backcross generations were tested. Neck-rot resistance was evaluated by assay of detached onion scales. Pyruvic acid content (PA) as an objective measure of pungency was determined by spectrophotometric analysis, and total soluble solids content (SS) was determined by measurement of refractive index.

In the diallel cross, there was a moderate positive correlation between SS and PA, a low negative correlation between PA and neck-rot disease index (DI), and a medium negative correlation between SS and DI. Estimates of

general combining ability were highly significant for all three traits. General combining ability was more important than specific combining ability. No heterosis effects were found in SS, but small heterosis effects for DI and PA were found in some F_1 hybrids.

Analysis of segregating generations of individual crosses between neck-rot susceptible, low SS, low PA parents x neck-rot resistance, high SS, high PA parents indicated that additive gene action predominated but with some dominance, and that PA was also subject to epistatic gene effects. Broad sense heritability estimates were medium for SS and PA for crosses in which parents differed strongly for these characteristics. Low heritability was found in a cross in which parental differences in DI and SS were small.

Recurrent and mass selection would be effective in a breeding program for high pungency and high SS cultivars with neck-rot resistance. Use of the simple and rapid hand refractometer method to select high SS was effective in selecting high pungency and neck-rot resistant bulbs.

The Genetic Analyses of Neck-rot (*Botrytis allii* Munn) Resistance, Pungency and Soluble Solids Content of Onion (*Allium cepa* L.)

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IN DEDICATIONS TO:

Li-Chu Wu Lin, my wife

Yen-Yin Lin, my daughter

Chen-Yang Lin, my son

Dr. Mau-Yeong Lin, my brother

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I. INTRODUCTION

The onion (*Allium cepa* L.) is important as food or flavoring in nearly every nation of the world. In 1987, 25.2 million MT of onions where harvested from 1.7 million ha. Leading countries in bulb onion production were China, India, United States, USSR, Turkey and Japan (Food and Agriculture Organization, 1987). In the United States, this crop was reported to be the 4th important vegetable with a total value of 503 million dollars, the only vegetable crops exceeding this value were tomato, potato and lettuce (USDA Agricultural statistics, 1988). Several closely related *Allium* species, garlic (*A. sativum*), leek (*A. ampeloprasum*) and Japanese bunching onion (*A. fistulosum*) are also important food crops.

Onions are consumed either as mature bulbs or immature plants. Mature bulbs may be used directly after harvest from the field or may be stored for up to six months or more. In the United States, 73% of the onions produced were stored prior to use (USDA Agriculture statistics, 1988). Mature onion bulbs, either freshly harvested or stored, may be used raw or cooked for culinary purposes, commercially

canned or frozen alone or in mixed vegetable products, or dehydrated. Sweet, mild onions are favored for fresh raw uses, while pungent types are preferred for cooking, processing, or dehydration.

Pungency is a distinct cultivar characteristic, though little genetic information is available. Mildly pungent onions have been reported to be associated with poor keeping quality and with low dry matter content (Foskett, 1950). The percentage of neck-rot diseased bulbs was significantly higher in the mildly pungent than in the strongly pungent varieties (Owen et al., 1950; Hatfield et al., 1948). Platenius and Knot (1941) reported that total dry matter content reflects pungency to some extent; and varietal differences had the most pronounced influence on pungency.

In the United States onion neck-rot disease occurs in every onion growing district (Gunkel et al., 1971). It causes 3% to 8% losses of onions received in metropolitan New York (Ceponis, 1981). Annual crop losses of 10% have been reported for Great Britain (Derbyshire, 1973), and 10-20% for the Netherlands (Tichelaar, 1967). Onion neck-rot is the most serious disease of storage onions in Norway (Vik and Astvei, 1984).

Because of the relationship between low pungency, low dry matter, and susceptability to Botrytis neck-rot, the development of cultivars with low pungency and reduced neck-rot susceptibility is a difficult challenge for onion

breeders. Improved testing methods for neck-rot resistance and additional information on the inheritance and relationship of these traits is needed. Therefore, the present study was undertaken to:

1. Improve scale inoculation methods to provide a more precise and reliable screening for neck-rot resistance in onion bulbs.
2. Investigate the inheritance of variation in neck-rot resistance, pungency and soluble solids content among several inbred onion lines.
3. Study the relationships among pungency, soluble solids, and neck-rot resistance in this material.

II. LITERATURE REVIEW

ONION NECK-ROT DISEASE

The first descriptions of neck-rot of onion were published in Germany by Soraucer in 1876, in the United States by Halsted in 1890, and in England by Massee in 1894 (Munn, 1917). Munn found neck-rot repeatedly in New York and Michigan from 1913 to 1916. He identified the causal organism of neck-rot as Botrytis allii Munn. His identification was subsequently confirmed by workers in many countries (Wallace, 1945; Tichelaar, 1967; Lawes, 1967).

Walker (1926) distinguished three species of Botrytis, each of which may incite a neck-rot in onion bulbs. Because the three species produce diseases differing somewhat in symptoms, they were given different common names. Gray-mold neck-rot, caused by B. allii, is characterized by heavy and prompt production of a gray conidial mass upon the decaying host tissue. B. allii is the most common and important species which causes neck-rot of onion. Mycelial neck-rot, caused by B. byssoidea, is characterized by a predominance of mycelium and a scarcity of conidia on diseased tissue. Small sclerotia neck-rot, caused by B. squamosa, is characterized by the appearance of small sclerotia upon affected scales. B. squamosa is also the causal organism of Botrytis leaf blight of onion (Hancock, 1963).

There are a number of common names, such as gray-mold,

storage rot, bulb-rot, and neck-rot, applied to the disease caused by the fungus B. allii. Of these, the name neck-rot is most descriptive of the disease and is the name more readily recognized by growers (Munn, 1917).

The fungus B. allii belongs to sub-division Deuteromycetes (the imperfect fungi). It produces conidia and sclerotia which are infecting spores and resting structures, respectively. Sclerotia germinate by hyphae which form conidiophores. Conidiophores are short, erect, branching, septate, and bear conidial clusters. Conidias are ellipsoid, slightly tapering at both ends, and are attached to the vesicles in small clusters.

The symptoms of onion neck-rot disease

The first symptom of the disease is the softening of the affected neck scale tissue which takes on a sunken, cooked appearance with a definite margin between the diseased and healthy tissue. As mycelial growth increases in the older diseased area, the tissue becomes grayish in color and later a dense, grayish, cottony growth of the fungus appears on the surface of the scale. Infection progresses rapidly down the scale and somewhat slowly from scale to scale. Under humid conditions, conidia production is prompt and a dense layer of gray mold appears. This mold consists of short conidiophores. The powdery mass of spores can serve to spread the fungus for considerable distances.

Then, small, black, and kernel-like compacted masses of mycelium, called sclerotia, appear in older decayed tissue. The watery decayed tissue desicates rather promptly, and eventually the whole bulb may become mummified. The fungus is still active in this state and is a potential hazard to growing or stored crops (Munn, 1917; and Walker, 1926).

Infection of bulbs and growing plants

Infected seeds have been shown to be a source of B. allii inoculum. Bochow and Mosallamy (1979) reported that as many as 70% of the seeds were infected in some Dutch onions. The fungus invaded the tip of the cotyledon from the attached seed coat. The mycelium then progressed downward in the leaf tissue, producing conidiophores in plants without symptoms. Therefore, infected and healthy plants were indistinguishable.

Infection of bulbs occurs during the harvest period. The succulence of the neck tissue at harvest time is important in determining the amount of infection. If bulbs mature well during dry weather before harvest occurs, the chances of infection are greatly reduced (Walker, 1925). The greatest epidemic development of neck-rot occurs when cool, moist weather prevails for some days previous to and more or less frequently after harvest. Infection and post-infection decay of bulbs are clearly favored by temperatures between 15° and 20° C and high humidity (Munn, 1917; Owen et

al., 1950; Walker, 1926).

In latent infections of green leaves, the fungus remains quiescent within the epidermis and invades the mesophyll when leaves senesce or become necrotic (Tichelaar, 1967; Segall et al., 1960). Maude and Presly (1977a) found that infection occurs more frequently at the leaf tip of onion plants. In most plants, the infected leaves ultimately decay and the fungus remains on the leaf base which forms the wrapper leaves surrounding the onion neck and penetrates directly into the interior neck tissue. Thus the fungus and symptoms appear on the neck of the onion bulb (Maude and Presly, 1977b).

Control of the disease

Control by drying the onion crop after harvest either in the windrow or by artificial heat immediately after lifting is effective. Because B. allii does not invade dry onion neck tissue, rapid drying of the neck tissue can prevent spread of the fungus into the bulb (Harrow and Harris, 1969).

It has been found that field curing and artificial drying are very successful in reducing damage due to neck-rot, and that bruising of the bulb increases the incidence of storage rot (Hoyle, 1948). Infection may occur through wounds on any part of the bulb, and careful handling to avoid unnecessary bruising can reduced the disease (Vaughan

et al., 1964).

Avoidance of planting related crops in rotation (Presley, 1984), low temperature, and well ventilated conditions of the storage house are possible methods to control or decrease the losses from this disease (Walker, 1926).

Presley (1977) reported that dusting seed with the systemic fungicide benomyl can reduce the average neck-rot incidence in stored bulbs from 26% to 3.8%. Tichelaar (1967) also found that treating infected onion seeds with benomyl can greatly reduce the level of neck-rot. In Britain, benomyl seed treatment has remained partly effective and its effect has been improved by the practice of growing onions in a long crop rotation (Maude, 1982). Munn (1945) and Groenendijk et al. (1962) reported that there are conspicious differences in the susceptability to B. allii among onion cultivars, and that white onions are more susceptible than yellow or red onions. Miyaura, Shinda and Gabelman (1985) suggested that resistance to neck-rot was obtainable through selection in self-pollinated progenies. Breeding resistant cultivars appears to be a promising method to control this disease.

Methods of testing for neck-rot resistance

Groenendijk and Petiet (1962) in the Netherlands developed a testing method which involves cutting off the

foliage near the neck of onion bulb and spraying with a spore suspension of B. allii. They found that there is a difference in susceptability in Dutch onion cultivars as well as in foreign onion materials. Van De Meer (1970) inoculated seedlings, detached leaves, and bulbs to test for neck-rot resistance. He reported that the bulb test appeared to be the most suitable because of its reliability and the possibility of carrying out the test at any desired period in autumn and winter. It was also better suited to repeated testing and appeared to be more effective than the method of Groenendijk and Petiet.

Vik and Astvei (1984) applied the bulb testing method of Van De Meer in an onion breeding program and found that there was no clear cut or specific resistance among cultivars. They suggested that neck-rot resistance as determined by this method is a quantitative character, which shows continuous variation and is in part fixable by selection. They concluded that inbreeding and selection within resistant populations can achieve a marked reduction in disease incidence.

Currah and Maude (1984) demonstrated that spraying seedlings with conidia was very destructive. They developed a non-destructive method in which leaf segments or leaf discs were inoculated individually with a drop of spore suspension, and found that A. fistulosum was more resistant than A. cepa to B. squamosa.

Miyaura, Shinda and Gabelman (1985) developed an inoculation method, using a drop of spore suspension placed on the inner site of a rectangular scale and incubated at room temperature. They divided the onion bulbs into resistant and susceptible groups after scale tests and compared their offspring performance. They found that the mean disease indices of selfed progeny derived from resistant bulbs tend to be lower than the mean indices for all the self-pollinated progeny derived from susceptible bulbs. They suggested that the heritable resistance to onion neck-rot can be obtained by selection through artificial scale test methods.

SOLUBLE SOLIDS CONTENT

Bacon (1957) reported that the major constituent of soluble solids content of the onion bulb consists of fructose, glucose, sucrose and a series of oligosaccharides. The oligosaccharides are mainly non-reducing sugars. Chain-length of the oligosaccharides does not exceed eight.

Birth and Dull (1985) examined the composition of low dry matter (Granex) and high dry matter (Creole) types of onion. They found that fiber, starch and sugars account for 85.8% and 82.2% of the dry matter in Granex and Creole onion respectively. These values are in agreement with those reported by Darbyshire and Henry (1979) who also reported an association of soluble oligosaccharides with high

percentages of dry weight in onion.

Dry matter and soluble solids measurement

A precise study of dry matter in onion bulb would require the use of oven drying techniques; this would make the study very time consuming and destroy the onion bulbs. Mann and Hoyle (1945) studied the use of the refractometer as a means of determination the percentage dry matter content of onion bulb. They found that the refractive index of the juice of onion bulbs (expressed as % concentration of sucrose solution) was closely correlated ($r = 0.91$) with the percentage dry matter as determined by oven drying techniques. They suggested that one can select for high dry matter on this basis without knowing the actual percent dry matter of the bulbs by using the regression line of % dry weight of the whole bulb on the refractometer reading.

Foskett and Peterson (1949) and Warid (1952) have confirmed these findings. They stated that estimation of percentage of dry matter of onion bulb by refractometer is a rapid method, and that the sample bulb may be used for seed production in the breeding program.

Since the dry matter content is equivalent to the total yield of the final dehydration product (McCollum, 1968), onion cultivars having a high percentage dry matter are more efficient to dehydrate. However, existing cultivars with high dry matter produce much lower yield of bulbs than do

the Sweet Spanish types which have a low percent dry matter.

Grieg (1965) and Owen (1961) reported that the white Sweet Spanish type onions are not preferred for dehydration because its dry matter content is not high. An ideal cultivar for dehydration purposes would be one which has the potential of high yield in its area of adaptation and at the same time has a high dry matter content.

Dry matter and storage quality

Foskett and Peterson (1950) studied the relation of dry matter content to storage quality in open pollinated hybrid cultivars. They found a decided tendency for cultivars having a high percentage of dry matter to be less likely to sprout during storage than those with low dry matter. Keeping quality was generally correlated with percentage dry matter; bulbs of high soluble solids content being the best keepers. They suggested that soluble solids measurement may be useful as a rapid means of roughly classifing cultivars and inbreds for storage quality.

Jones and Bisson (1934) found that mild onions and those of rather poor storage quality have the highest moisture content; whereas those that are the most pungent and keep best in storage have the lowest moisture content. The difference in percent of dry matter between cultivars is of considerable practical importance to those interested in the dehydration products of onions.

Inheritance of soluble solids

McCollum (1968) studied the heritability of soluble solids and its correlation with bulb size and shape in white Spanish onion. He reported that the heritability of soluble solids was high and there was a negative genetic correlation between soluble solids and bulb size.

Warid (1952), using a components of variance method on parents and F_2 generation by crossing high solids (about 16%) and low solids (about 6%) cultivars, obtained 71% heritability in green house populations and concluded that 4-10 gene pairs for soluble solids and partial dominance of low solids were involved in the cross.

Owen (1961) studied the segregation of soluble solids genes and postulated that cumulative gene action and a relatively small number of genes are involved in the inheritance of solids; and concluded that selection to change soluble solids content of onions would be effective.

PUNGENCY OF ONION BULB

Allium species are consumed as foods mainly because of the volatile flavor. It is known that the volatile components of several Allium species are rich in sulfur compounds (Carson, 1961). The flavor is formed when the cell of the storage scales are disrupted by comminution. Much of the flavor and odor of onions arise as the result of

conversion of precursors (S-substituted cysteine sulfoxide derivatives) to unstable alkyl sulfenic acid by an allinase enzyme present in onion (Schwimmer et al., 1960; Kupiecki 1960).

The major precursor of onion flavor is S-(1-propyl)-L-cysteine sulphoxide; the corresponding S-1-methyl- and S-1-propenyl-L-cysteine sulphoxide are present in small quantities (Virtanen, 1959; Lancaster and Kelly, 1983). On injury of the onion tissue, the precursors undergo the attack of allinase enzyme with production of equimolecular quantities of thiopropanal S-oxide, pyruvic acid and ammonia (Schwimmer and Weston, 1961; Freeman, 1975).

The initial product, 1-propenyl-sulphenic acid, which is considered to be an unstable intermediate, is then converted to a more stable sulfur containing product, thiopropanal sulfuroxide, which imparts the characteristic pungency.

Matikkala (1967) reported that methyl and propyl thiosulphenic acid will react with thiamine to give rise to allithiamine analogs; and with N-ethyl maleimide after appropriate extraction procedure and heating, to give rise to families of alkyl mono-, di- and trisulfides which have been identified after separation by gas chromatography (Carson 1961). In addition, the following volatile sulfur-containing compounds have been reported to be present in onion volatiles: n-propanethiol, n-propyl-thioaldehyde,

hydrogen sulfide and sulfur dioxide (Niegish and Stahl, 1956).

Methods of measurement of onion pungency

Platenius and Knot (1941) mentioned that the measure of pungency by taste test is very inaccurate because of the accumulative effect of successive tasting. A more satisfactory measure of pungency in onion became available through the development of a chemical method which made it possible to express the result in numerical values.

The mechanism of production of volatile flavor components suggests several approaches towards the objective evaluation of pungency of onion. The most direct over-all approach would be the determination of volatile sulfur. This was used in the pioneering work of Platenius (1935), who determined sulfur in a distillate after acid hydrolysis of the onion at high temperature. Currier (1945) improved this method by using lower temperature and by converting sulfur eventually to methylene blue, thus getting a colorimetric determination of sulfur.

Luke (1971) developed a thin-layer chromatography method for evaluation and separation the flavor compounds of onion juice. He mentioned that the principal advantage of the method is that it can measure the relative concentration of other products of the action of allinase on the flavor precusors.

Freeman and Mossadeghi (1971), using gas-chromatographic methods to analyse flavor and odor compounds, indicated that this method may alter the amounts of flavor components due to the instability of 1-propenyl compound at the high temperature.

Freeman and Whenham (1975), using a spectrophotometric method to determine the thiopropanal S-oxide, found that there was a highly significant positive correlation ($r = 0.99$) between thiopropanel S-oxide and pyruvate concentration but that thiopropanel is unstable in distillation.

The presence of relatively large amounts of pyruvic acid in onions was first detected qualitatively by Bennet (1945). Morgan (1946) proved its presence by isolation pyruvic acid with 2,4 dinitrophenyl hydrazine (DNPH) from an unheated macerate and demonstrated that it arises enzymatically from precursors.

Schwimmer and Weston (1961) developed a very rapid and relatively simple method to determine the amount of pyruvic acid. They found at least 95% of maximum of pyruvic acid developed within 6 minutes after begining of the comminution process, and the amount of pyruvic acid developed to bear a reasonable relation to the degree of onion pungency.

Schwimmer and Guadagni (1962) also reported a highly significant correlation ($r = -0.97$) between the amount of enzymatically developed pyruvic acid in the juice of

comminuted onion and the olfactory threshold concentration of the juice. They suggested that determination of stable end-products of pyruvic acid is a fairly reliable, simple, and convenient assay of onion pungency intensity.

Factors affecting the pungency of onion

The pungency of onion is influenced by soil and other ecological factors as well as genetic factors. It has been found that soil type, water content, and nutrition affect pungency. Onions grown on a peat soil were more pungent than those grown on a sandy soil, while those grown on a loam or sandy loam were intermediate in pungency (Platenius, 1941). Freeman and Mossdeghi (1973), by means of greenhouse experiments in sand or solution culture, found that the most striking effect of extreme sulfur deficiency was the complete absence of pungency. Kumar and Sahay (1954) also found that onions increase in their volatile sulfur content and in pungency when large quantities of elementary sulfur were applied to the soil. They postulated that a certain level of sulfur nutrition was require for the synthesis of the flavor precusors.

Another factor which has a marked influence on onion flavor is the water content of soil in which onions are grown. An abundant supply of water in the growing stage tends to result in large bulbs but relatively lacking in flavor, whereas those grown with restricted amounts of water

may be smaller and less attractive in appearance but are often richer in flavor (Freeman and Mossdeghi, 1973).

The most important factor affecting onion flavor intensity is the genotype of onion cultivars. Freeman and Mossadeghi (1971) found that an increase in the sulfur concentration in solution culture tends to increase the flavor intensity progressively up to the genetically controlled limit. Lancaster (1984) found that the proportion of flavor precursor changes with cultivars. Schwimmer and Weston (1961) also demonstrated that the amount of pyruvic acid produced from mature onion bulbs varied between 4 and 20 µ mole per gram of bulb and appeared to depend on the pungency strength of the onion.

Inheritance of onion pungency

Pal and Singh (1987) studied the genetics of pungency (pyruvic acid) in onions by analyses of parental and F_1 data from a diallel cross among 8 inbred lines. They reported that pyruvic acid was controlled by both additive and dominance gene effects, the former being more important. They suggest that it should be possible to improve the character both by heterosis breeding and by conventional breeding methods.

Correlations of pyruvic acid, soluble solids and neck-rot disease index

The relationship between solids and odor was studied by Schwimmer and Guadagni (1962). They found that there is a medium correlation ($r = 0.57$) between the two traits. Platenius and Knot (1941) also reported that total solids content reflects pungency to some extent. Owen *et al* (1950) studied the pungency, color and moisture supply in relation to disease resistance in the onion. They reported that the onion neck-rot disease was more severe on mild than on pungent cultivars. In the mild class, there was no difference between colored and white cultivars, while in the pungent class, the colored cultivars had significantly lower disease indices than white cultivars.

III. MATERIALS AND METHODS

PLANT MATERIALS

Ten diverse and distinct inbred lines of onions (A. cepa L.) listed in Table 1 with original sources and types, were selected from the breeding collection of long day type onions of Sunseeds Company at Brooks, Oregon for use as parents in these studies. The lines represented a range of types that vary in pungency and soluble solids content. Each line had a background of several generations of inbreeding.

Nine of the lines were used as parents in a diallel cross. Five lines were chosen as parents for individual crosses for analyses of segregating generations.

Crossing and seed production methods

All parental stocks used for the diallel analysis were inbred onion lines and had available cytoplasmic-genic male sterile companion lines from the inbred nursery of Sunseeds Company onion breeding program. Cross pollinations were made in the Summer of 1986 by placing male sterile plants of the female parents in screen isolating cages together with male fertile plants of a single male parent in each cage. Honey bees were used as pollinators. In this manner, hybridizations were made among the nine parents to produce

the 36 possible F_1 hybrid progenies, without reciprocals, for the diallel analysis.

Table 1. Inbred lines used as parents in a diallel cross and analyses of generations.

Inbreds	Abbreviated designation	Original[z] source	Type[y]	Soluble solids content	Pungency
B6693	B6693	A & B & C	Y	high	high
MSU 8155	M8155	A & C	Y	medium	medium
MSU 5718	M5718	A & C	Y	high	medium
PG-1b	PG1b	D	X	low	low
P6502	P6502	D	X	low	low
W407	W407	E	Y	low	medium
W202	W202	E	Y	medium	medium
W420	W420	E	Y	high	high
Ia 163	Ia163	A & F	Y	low	medium
WSS D10-1b	D10-1b	G	W	low	low

[z] Source:
A = U. S. Department of Agriculture.
B = Wisconsin Agricultural Experiment Station
C = Michigan Agricultural Experiment Station
D = Idaho Agricultural Experiment Station
E = University of Wisconsin
F = Iowa Agricultural Experiment Station
G = Sunseeds

[y] Type:
W = White Sweet Spanish
X = Yellow Sweet Spanish
Y = Yellow Globe

For the study of segregating generations and generation means analyses, bulbs of eight parents were planted in April 1986. The 112 possible cross combinations, including reciprocal crosses, were attempted. Seeds of the F_1 generation were obtained by hand emasculation of female parents before stamen dehiscence and pollination by hand in June and July 1986. Forceps used in pollination were sterilized with alcohol to avoid possible contamination. The F_1 seeds were successfully obtained from 70 crosses, from which six were eventually chosen for the genetic study. The two parents of each cross were selfed by using flies as pollinators in small cages.

To obtain F_2 seed and make backcrosses, F_1 and parent seeds were planted in the greenhouse in September 1986, vernalized in pots, and flowered in June and July 1987. Selfing of the F_1 and parent plants was done on an individual plant basis, using flies as pollinators. Additional F_1 seeds and backcrosses were obtained by hand emasculation, and pollination by hand or by flies. To avoid contamination, umbels of female plants were covered with paper bags before pollination.

Field planting and bulb production

Production of test bulbs for the diallel was done in the field on Sunseeds Research Station near Brooks, Oregon. Seeds of the 36 F_1 progenies and nine parents were planted

in April 1987 in a randomized complete block design with three replications. In each block, each genotype was planted in a 2-row plot, 6 m long with rows 0.5 m apart. Seedlings were thinned to stand 7.6 cm apart in the row. Cultural methods were typical of those used in commercial onion production in western Oregon, and included sprinkler irrigation as needed and a biweekly insecticide and fungicide spray.

A random sample of 20 bulbs of each genotype from each block was harvested in late September 1987, to provide 60 bulbs of each genotype to test for neck-rot disease index (DI), pyruvic acid content (PA) and soluble solids content (SS). After harvest, all of the bulbs were stored in a cold storage room at 5° - 10° C before testing.

To produce bulbs for the generations analyses, seeds of six generations (Table 2) of six crosses were planted in the greenhouse on March 19, 1988. Plants were grown in seedling trays for six weeks, then transplanted to the field. A randomized complete block design with four replications was used. Rows were 51 cm apart with 9 cm (3.5 inches) between plants. In each replication, the six generations of a single cross were randomized in one row. Bulbs were dug on September 15, field cured for three weeks, then cleaned and stored at 5° - 10° C. DI and SS tests were conducted in October 1988 to January 1989. Two crosses (W420 x Pg-1b and W420 x B6693) were selected for PA analyses in February to

March 1989. The number of bulbs per sample for each generation of the six crosses is summarized in Table 2.

Table 2. Number of onion bulbs of parents and derived generations used for testing for onion neck-rot disease index, soluble solids content and pyruvic acid content in the analyses of generations.

Crosses	Generations[z]					
P_1 x P_2	P_1	P_2	F_1	BC_1	BC_2	F_2
	Number of Bulbs					
W420 x Pg-1b	64	54	49	64	45	98
W202 x D10-1b	64	63	52	59	29	95
W420 x D10-1b	64	64	12	64	55	95
B6693x Pg-1b	63	64	25	64	64	116
W420 x B6693	60	46	62	62	62	107
W407 x D10-1b	60	49	39	59	26	95

[z] P_1 = more neck-rot resistant, higher soluble solids, more pungent parent. P_2 = less resistant, lower soluble solids, less pungent parent. BC_1 = backcross of F_1 x P_1. BC_2 = backcross of F_1 x P_2.

PRELIMINARY INOCULATION METHOD EXPERIMENTS

A group of initial experiments were conducted in the winter of 1986 to test and refine several aspects of the neck-rot disease resistance tests. Three long-day type inbred lines, which represent a range in expression of neck-rot resistance and susceptability were chosen for this study. Bulbs of resistant W420 and M1459 and susceptible W101 inbreds were grown on the Sunseeds Company farm at Brooks and harvested in August, 1986. Random samples of 20 bulbs of each line were saved for each of the preliminary experiments, described below.

Epidermal removal test. In this test, scales with the inner epidermis removed were compared with scales with the epidermis intact. For each treatment, three pieces of scales were cut from the 2nd layer, upper section of the bulbs, inoculated with a 1.0×10^5/ml spore concentration, and incubated at 20° C for six days.

Spore concentration test. Four spore concentrations, 1.2×10^6/ml, 2.4×10^5/ml, 2.2×10^4 /ml and 2.2×10^3/ml, of *B. allii* were compared, using the 2nd layer of the upper section of the bulbs with one drop of inoculum for each contentration. Scales were incubated at 20° C for six days.

Water drop test. After inoculation with one drop of a spore suspension (1.0×10^5/ml) on each scale, sterilized water was added to the inoculum to increase free water

content. Treatments consisted of the control (no water drop added), one drop of added water, and two drops of added water. Three scale pieces were cut from the 2nd layer of the upper section of the bulbs for each treatment and incubated at 20° C for six days.

Incubation temperature test. After inoculation with a standard spore suspension (concentration 10^5/ml) and the addition of one drop of water, scales were incubated at 20° C and 25° C for six days. Scale pieces were cut from the 2nd layer of the bulbs, five pieces for each temperature treatment.

Scale layer test. To determine the best scale layers to use in neck-rot resistance tests, scale pieces were cut from five successive layers of the onion bulbs, from the outermost fleshy layer, designated layer 1, to an inner layer designated layer 5. From each layer of each bulb, five rectangular scale pieces were cut from the upper section of the bulbs and tested with the standard inoculation method.

Bulb section test Bulbs were divided into upper, middle, and bottom sections. From each section, five scale pieces were cut from the 2nd layer for inoculation and test with the standard inoculation method.

PRELIMINARY SOLUBLE SOLIDS AND PYRUVIC ACID TESTS

For a trial analysis of SS done in October 1988, bulbs of W420 and W407 were harvested from the field. Bulb production was as described in previous experiments. Each bulb was cut into upper and lower sections. Sample scale pieces were then cut from each of five layers from each of the upper and lower sections of 20 bulbs for each inbred line. Two scale pieces from the 10 sampling sites of the onion bulb of each inbred were tested for total SS with a hand refractometer described on the pages following.

In winter of 1987, a trial analysis of PA was conducted to determine the best scale layers for PA determination. Bulbs of W420 and W407 were harvested from the field in the fall 1987. Scale layers 1-6 with the outer layer designated 1 were compared, using the PA analyses described on the pages following. For each layer, scales from five bulbs were mixed together as one sample for the analyses. Five samples of five bulbs each, randomly selected, were analysed for each inbred line.

LABORATORY ANALYSES

Neck-rot resistance tests

A culture of *B. allii* was provided by the plant pathology lab of Sunseeds Company. The organism was maintained on potato dextrose agar (PDA). New cultures were

started every two months and incubated at 20° C. Spores of B. allii were harvested from a new heavily sporulated culture by adding 20 ml of sterilized water to the petri-dish and loosening spores by slight rubbing with a flamed scalpel. Mycelium and spores were blended for 30 seconds to get an even spore suspension. Spore concentration was adjusted to 10^5-10^6 spores/per ml. Then, 50 mg of the antibiotic Cabenecilin were added to the spore suspension to supress bacterial contamination.

Before scale pieces were cut from onion bulbs, the dry scales were removed and the bulb surface was sterilized by spraying 75% with ethyl alcohol. The inner epidermis was removed from the scale pieces. Two rectangular scale pieces (2 x 1.5 cm) were cut from each of the second and third scale layers of each bulb.

Scale pieces were placed in a 32cm x 24cm x 10cm plastic box that had been previously sterilized with alcohol. A piece of blue blotter paper was placed in the bottom. The paper was moistened by adding 55 ml of sterilized water to each box to provide high humidity.

Neck-rot resistance was evaluated by the method of Miyaura, Shinda and Gabelman (1985). Each piece of scale was inoculated with one drop (about 0.04 ml) of spore suspension on the center of the scale surface. One drop of sterilized water was added. After inoculation, the box was covered and incubated at 20° C for six days. Each

individual scale piece was evaluated using a neck-rot disease index (DI) based on the degree of mycelium growth and sporulation and scale damage as follows:

Disease index	Description
0	No visable mycelium growth; or scale damage.
1	Very little mycelial growth; the diameter of mycelium less than 0.5 cm; scale becoming water soaked.
2	Moderate mycelial growth; the diameter of the mycelium more than 0.5 cm; no sporulation; scale watersoaked.
3	Heavy mycelial growth; little sporulation; scale becoming soft.
4	Heavy sporulation; scale totally broken down (rotten).

Total soluble solids measurement

Two scale pieces were cut from the 2nd and 3rd layers of the upper section of the onion bulbs. These two rectangular scale pieces were squeezed with a hand garlic press, and the juice dropped directly onto a hand refractometer. The SS of each bulb was read under light. The refractometer and garlic press were washed with distilled water in preparation for the next sample (Mann and Hoyle, 1945).

Pyruvic acid measurement

The determination of PA released after blending onion scale flesh with water was used as a measure of pungency (Schwimmer and Weston, 1961). After removal of the true stem and the dry outer scale, half to one third of the tissue of the bulb was weighed and placed in a mason jar with an equal weight of distilled water (1 ml water/ per gram of onion tissue). The tissue was blended 40 seconds. After 12 jars had been blended, samples were let stand 10 minutes to allow releasing of PA. The onion juice was then filtered into a test tube through #4 filter paper.

Using an automatic pipette, 2 ml of filtrate was transfered into a volumetric flask, and then diluted to 100 ml with distilled water. The flask was then shaken. Two ml of the dilute solution were then placed in a test tube to which had been added 1 ml of DNPH (0.0125% 2,4-dinitro-phenyl hydrazine in 2 N HCl). A rack containing 12 tubes was placed into a 37° C water bath. After 10 minutes, the reaction was stopped by adding 5 ml of 0.6 N NaOH to each tube. The samples were then allowed to stand for five minutes for color development.

The absorbance of each sample was measured with a spectrophotometer set at 420 nm, using a reagent blank set at 0 absorbance (2 ml water + 1 ml DNPH + 5 ml NaOH). A standard curve for calibration was obtained by using sodium

pyruvate as a reagent with gradient concentrations of PA. The absorbance was read to get a standard curve of PA for transforming the spectrophotometer reading into PA concentration for each onion sample.

DATA ANALYSES

Diallel cross

Individual F_1 family means of DI, PA, and SS were compared with their respective parents. The LSD values were based on error mean squares (EMS) obtained from the initial analyses of variance of the diallel cross family means (parents and F_1's). The standard error of the difference between an F_1 progeny and common parent mean = $(2EMS/r)^{1/2}$, where r is the number of replications (Steel and Torrie, 1980). Heterosis effects (%) from the mid-parent (MP) were computed as $[(F_1 - MP)/MP] \times 100$. Because mid-parent values ($MP= 1/2(P_1 + P_2)$) are estimated with twice the precision of a family mean, the standard error of the difference between an F_1 and its respective mid-parent = $(3EMS/2r)^{1/2}$.

When the genotype effect was found to be significant, it was further partitioned into general and specific combining ability effects. Analyses of combining ability were made according to Griffing's model I, method 4 (Griffing, 1956). For this analysis, data from one complete set of F_1's, without parents or reciprocals, were utilized. All effects in the model except error were considered fixed.

Subsequent to the overall combining ability analyses, the general combining ability effect of the ith parent (g_i), the specific combining ability effect for each cross between the ith and jth parent (s_{ij}) and the variance of specific combining ability effects for ith parent (S^2_{si}) were computed using Griffing's (1956) formulas.

$$g_i = 1/p(p-2) \times (p X_{i.} - 2 X_{..})$$

$$s_{ij} = X_{ij} - 1/p-2 (X_{i.} + X_{.j}) + 2/(p-1)(p-2)X_{..}$$

$$S^2_{si} = 1/(p-2) \text{ Sum } (s_{ij})^2 - p-3/p-2 \times SS_e$$

The estimated mean squares analysis of combining ability of the three traits was derived as follow:

Source	DF	Sum of Square	Mean Square
General C.A.	p-1	SS_g	MS_g
Specific C.A.	p(p-3)/2	SS_s	MS_s
Error	m	SS_e	MS_e

Where $SS_g = 1/p-2 \text{ Sum } X_i^2 - 4/p(p-2) X_{..}^2$

$SS_s = \text{Sum } X_{ij}^2 - 1/p-2 \text{ Sum } X_{i.}^2 + 2/(p-1)(p-2)X_{..}^2$

The assumptions underlying the analyses as given by Hayman (1954) are:

1. Diploid segregation.
2. No difference between reciprocal crosses.
3. Independent action of non-allelic genes.
4. No multiple alleles.
5. Homozygous parents.

6. Genes independently distributed among the parents.

Generations means analyses.

The data recorded for each variable were used to plot frequency distribution histograms and curves to illustrate segregation patterns of each generation. The generation means were subjected to an initial analysis of variance. A significant F-test indicated genetic differences among generations. These differences were further analyzed in terms of gene effects. The steps were as follow:

First,the estimates of three parameters (mean, additive, and dominance effects) were made using the method proposed by Hayman (1958). A nonsignificant Chi-square test of the difference between observed and predicted means indicated that the variation among generation means is adequately described by this model. The estimates of mean effects (m), additive gene effect (a) and dominance gene effect (d) are as follow:

$$m = \{2E_2E_B\ (P_1+P_2+2F_1) + (E_P+2E_1)\ [E_BF_2+ E_2(B_1+B_2)]\} / 2E^2$$

$$a = \{2E_B\ (P_1-P_2) + E_P\ (B_1-B_2)\} / (E_P + 4E_B)$$

$$d = \{2E_2E_B\ (2F_1-P_1-P_2) + E_1E_B(2F_2-P_1-P_2)+ 2E_1E_2(B_1+B_2-P_1-P_2) + E_PE_B\ (F_1-F_2) + E_PE_2\ (2F_1-B_1-B_2)\} / E^2$$

$$E^2 = \{(E_P+2E_1)\ (2E_2+E_B) + 8E_2E_B\} / 2$$

Where P_1, P_2, F_1, F_2, BC_1 and BC_2 are the means of parents and progenies. E_P, E_1, E_2 and E_B are the error

variances of parents, F_1, F_2 and backcross populations.

The Chi-square (X^2) test for the additive-dominance model has three degree of freedoms and can be written :

$$X^2 = \{E_B(P_1+P_2+2F_1-4F_2)^2 + 2E_2(P_1+P_2+2F_1-2B_1-2B_2)^2 + (E_P+2E_1)\ (2F_2-B_1-B_2)^2\} / 4E^2 + (P_1-P_2-2B_1+2B_2)^2 / (2E_P + 8E_B)$$

If the chi-square value is significant, the additive-dominance model is inadequate and the full six parameter model is fitted. The estimated gene effects were calculated using the model derived by Mather and Jinks (1971). The information available from the means of generations derived from two inbred lines is contained in six parameters as follow:

Gene effect	Parameter
mean	m
additive	a
dominance	d
additive x additive	aa
additive x dominance	ad
dominance x dominance	dd

The perfect fit estimates of the six parameters are given by:

$$m = 1/2\ P_1 + 1/2P_2 + 4F_2 - 2BC_1 - 2BC_2$$

$$a = 1/2P_1 - 1/2P_2$$

$$d = 6BC_1 + 6BC_2 - 8F_2 - F_1 - 1.5P_1 - 1.5P_2$$

$$aa = 2BC_1 + 2BC_2 - 4F_2$$

$$ad = 2BC_1 - P_1 - 2BC_2 + P_2$$

$$dd = P_1 + P_2 + 2F_1 + 4F_2 - 4BC_1 - 4BC_2$$

Where P_1, P_2, F_1, F_2, BC_1 and BC_2 are means of parents, F_1, F_2 and backcross generations. Error variances for each parameter are calculated as follow:

$$\text{var } m = 0.25VP_1 + 0.25VP_2 + 16VF_2 + 4VBC_1 + 4VBC_2$$

$$\text{var } a = 0.25VP_1 + 0.25VP_2$$

$$\text{var } d = 36VBC_1 + 36VBC_2 + 64VF_2 + VF_1 + 2.25VP_1 + 2.25VP_2$$

$$\text{var } aa = 4VBC_1 + 4VBC_2 + 16VF_2$$

$$\text{var } ad = 4VBC_1 + VP_1 + 4VBC_2 + VP_2$$

$$\text{var } dd = VP_1 + VP_2 + 4VF_1 + 16VF_2 + 16VBC_1 + 16VBC_2$$

Where VP_1, VP_2, VF_1, VF_2, VBC_1 and VBC_2 are variances of parents, F_1, F_2 and backcross generations.

Phenotypic and environmental correlations among DI, PA, and SS were calculated from variance and covariance of the P_1, P_2, F_1 and F_2 generations with methods described by Cahaner and Hillel (1980). Environmental variance and covariance were estimated as suggested by Mather and Jinks (1977) in the following manner.

$$V_e = 1/4\text{Var } P_1 + 1/4 \text{ Var } P_2 + 1/2 \text{ Var } F_1$$

$$\text{Cov}_e = 1/4\text{Cov } P_1 + 1/4\text{Cov } P_2 + 1/2 \text{ Cov } F_1$$

Where V_e and Cov_e are estimates of the environmental variances and covariances. Var P_1, Var P_2, and Var F_1 are variance of the P_1, P_2, and F_1 generations, respectively; and

Cov P_1, Cov P_2, and Cov F_1 are covariances between two traits of the P_1, P_2, and F_1 generations, respectively. Environmental correlation (r_e) was estimated using the equation:

$$r_e = (Cov_e) / [(V_{e(i)}) (V_{e(j)})]^{1/2}$$

Where Cov_e, $V_{e(i)}$, and $V_{e(j)}$ are the estimated environmental covariance and variance of traits i and j, respectively.

Phenotypic correlations (r_p) were calculated as:

$$r_p = (Cov_{F2}) / [(V\ F_{2(i)}) (V\ F_{2(j)})]^{1/2}$$

Where Cov_{F2}, $V\ F_{2(i)}$, and $V\ F_{2(j)}$ are the covariance and variances in the F_2 generation of traits i and j, respectively.

Significance levels of r_p and r_e were determined from the tables for that purpose presented in Steel and Torrie (1980).

Broad sense heritability (h^2) was calculated by using the variance of parents, F_1 and F_2 populations. The estimates of broad sense heritability were made using the following formula suggested by Mahmud and Kramer (1951).

$$h^2 = [(V\ F_2 - V\ E / V\ F_2) \times 100$$

The $V\ F_2$ is the total variance (genetic variance plus non-genetic variance), and V E is the enviromental variance

(non-genetic variance). The enviromental variance was calculated from the variances of the non-segregating populations (P_1, P_2, and F_1) by the cube root of V P_1 x V P_2 x V F_1.

Deviations of F_1, BC_1, and BC_2 means of three traits from their respective mid-parent values were analyzed as a test of additive gene effects. The mid-parent values of F_1, BC_1, and BC_2 were determined using an additive model by taking the average of parents, F_1 and BC_1, F_1 and BC_2, respectively, using the formulae of Ali (1984), and Kim and Brewbaker (1977).

Deviation	Population	Standard error
F_1 - MP	$F_1 - (P_1 + P_2)/2$	$(MSE/n)^{1/2}$
BC_1 - MP	$BC_1 - (P_1 + F_1)/2$	$(10MSE/16n)^{1/2}$
BC_2 - MP	$BC_2 - (P_2 + F_1)/2$	$(10MSE/16n)^{1/2}$

IV. RESULTS AND DISCUSSIONS

PRELIMINARY INOCULATION METHOD EXPERIMENTS

The average DI of bulb scales was determined for scale layers 1 to 5. As shown in Fig. 1, susceptible inbred line W101 had a significantly higher DI in each layer than inbred lines W420 and M1459. The outermost and innermost scale layer produced the lowest and highest DI, respectively, with each of the inbreds. There was no significant difference between W420 and M1459 in DI from the 1st to 5th scale layer.

In inbred W101, scale pieces cut from the bottom section of the bulbs had a lower DI than the upper part (Fig. 2), but there was no difference between the upper and middle section. This indicated that the upper section of the bulb scale was more susceptible to infection by B. allii. There was no effect of scale position with W420 and M1459. Again, there was a strong difference between susceptible line W101 and the two more resistant lines.

Removing the inner epidermis of the scale resulted in a much higher DI (2.8) than in intact scales (0.7) in W101 (Fig. 3). In W420, the effect of scale epidermis removal was not significant. In M1459, removal of the scale epidermis caused a slight but significant increase in DI.

Incubation temperature of 20° C resulted in a distinctly and significantly higher DI in W101 than did 25°

C. Similar but less pronounced temperature effects were observed in W420 and M1459 (Fig. 4). The effect of temperature was significant in M1459, but not in W420.

The DI increased with the increase in spore concentration (Fig. 5). The DI of inbred W101 increased strongly and uniformly from a spore concentration of 10^3/ml to 10^5/ml, then made a small increase to 10^6/ml. In inbreds W420 and M1459, there was only a small increase in DI as spore concentration increased from 10^3/ml to 10^6/ml, except that W420 increased sharply from 10^5/ml to 10^6/ml. The biggest difference in DI of resistant and susceptible lines was about at 10^5/ml.

The addition of one drop of distilled water with one drop of spore suspension gave better differentiation of resistant and susceptible genotypes than did zero or two drops (Fig. 6). Increasing the water amount to two drops increased infection in the more resistant lines and slightly improved differentiation of W420 and M1459, but caused a slight reduction in DI of W101.

PRELIMINARY SOLUBLE SOLIDS AND PYRUVIC ACID TESTS

There was a tendency (not statistically tested) for SS to increase from the outer scale layer to the inner layer when layer 1 through 5 were compared (Fig. 7). The bottom section of the scale contained higher SS than did the upper section. Inbred W420 contained higher SS than W407, and the

effect of scale layer and upper and lower section was similar in these two lines. However, there was slightly better differentiation of cultivars at the second to fourth scale layers.

PA of onion flesh from different scale layers was measured and shown in Fig. 8. In inbred W407, there was a tendency for PA of the second and third scale layers to be lower than that of the outermost and of the innermost layer. However, in inbred W420 the 4th layer was highest in PA with the 6th layer lowest.

Each of the preliminary experiments provided information which should be useful in designing tests for DI, or determination of SS and PA. Generally, these tests showed that best differentiation of resistant and susceptible genotypes be obtained by:

(1) Testing scale layers 2-4.
(2) Testing scale pieces from the upper section of the bulb.
(3) Removing the epidermis from the scale to be inoculated.
(4) Incubating at a temperature of 20° C rather than 25° C.
(5) Using a Botrytis spore concentration of about 10^5.
(6) Adding one drop of distilled water with a drop of spore suspension.

Additionally, it was found that:

Scale layers 2-4 gave the best determination of SS.

Scale layers 1-5 gave the best differentiation of PA.

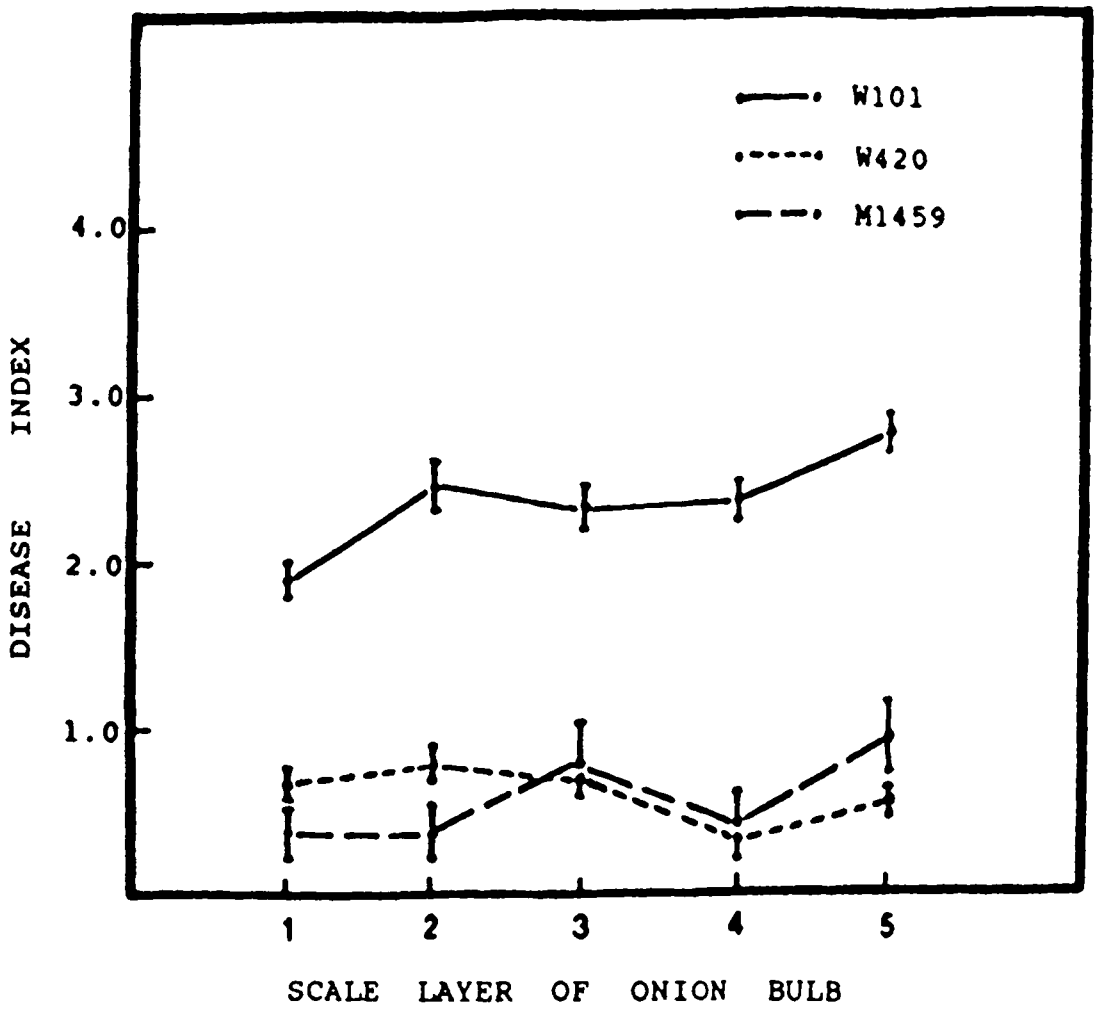

Figure 1. Neck-rot disease index of scale layers 1 (outermost) to 5 (innermost) of three onion inbred lines, vertical bars show the SE for each mean.

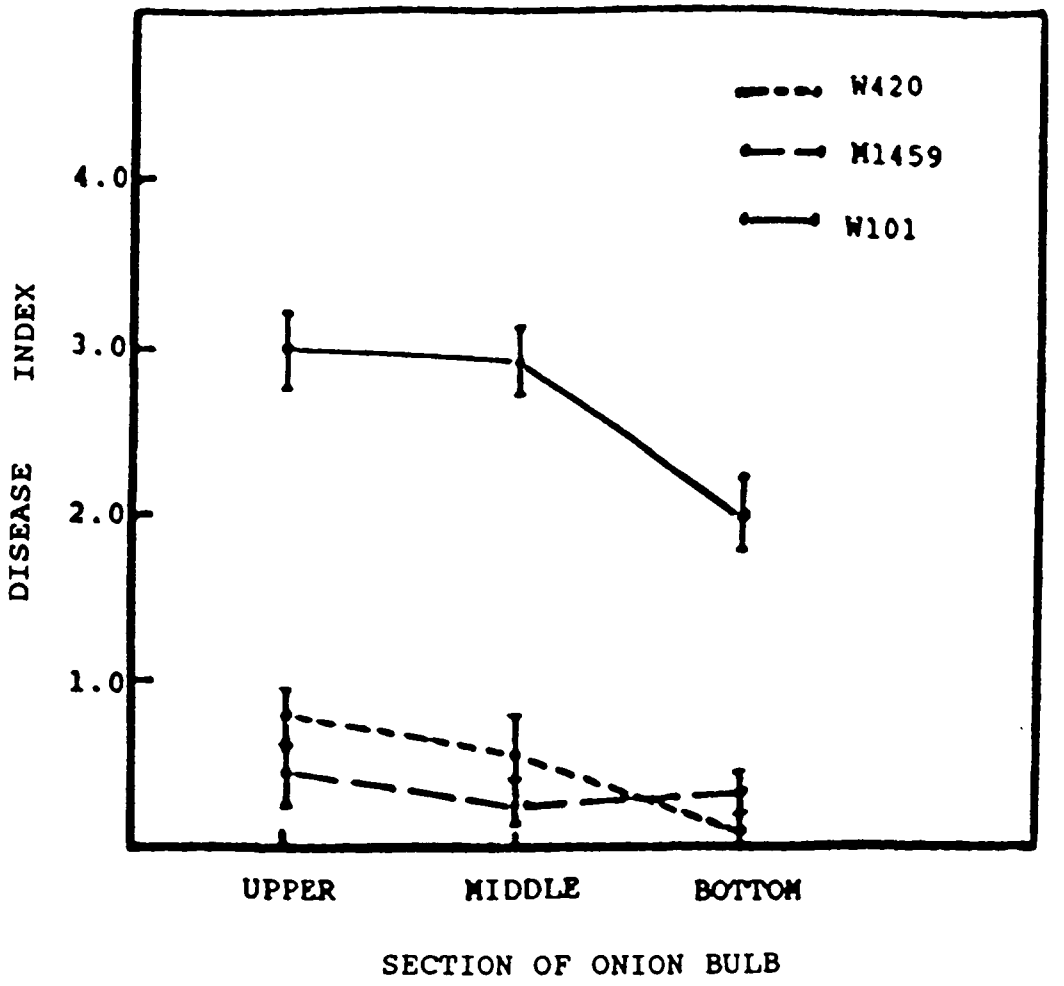

Figure 2. Neck-rot disease index of scale pieces obtained from the upper, middle and bottom section of the bulbs of three onion inbred lines, vertical bars show the SE for each mean.

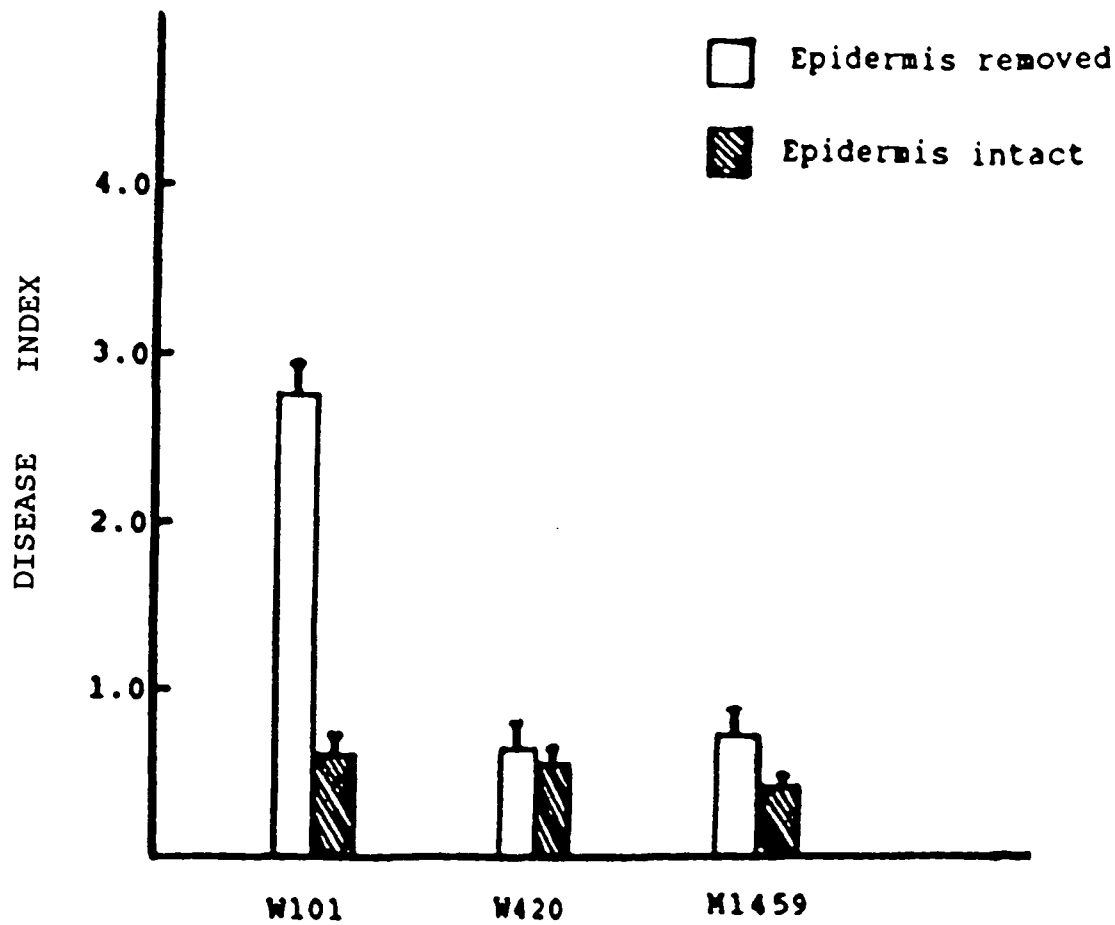

Figure 3. Effect on neck-rot disease index of removal of inner epidermis of the second scale layer in three onion inbred lines, vertical bars show the SE for each means.

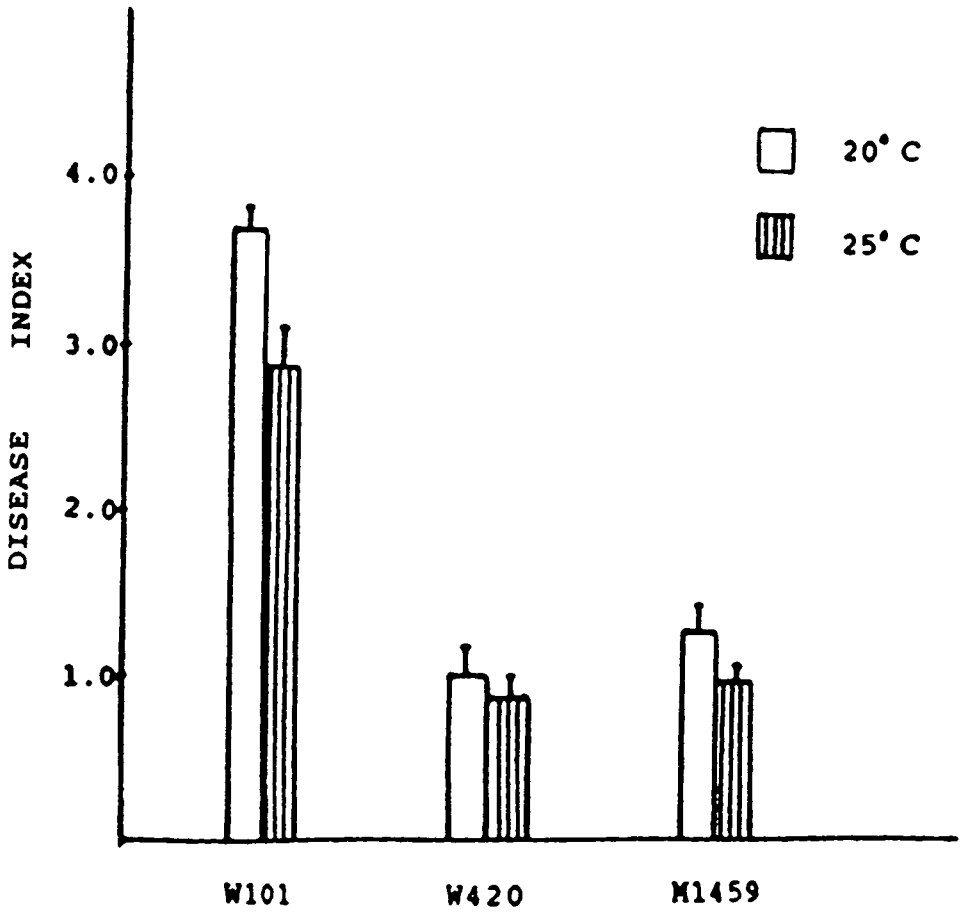

Figure 4. Effect of incubation temperature on the neck-rot disease index of the second scale layer of three onion inbred lines, vertical bars show the SE for each mean.

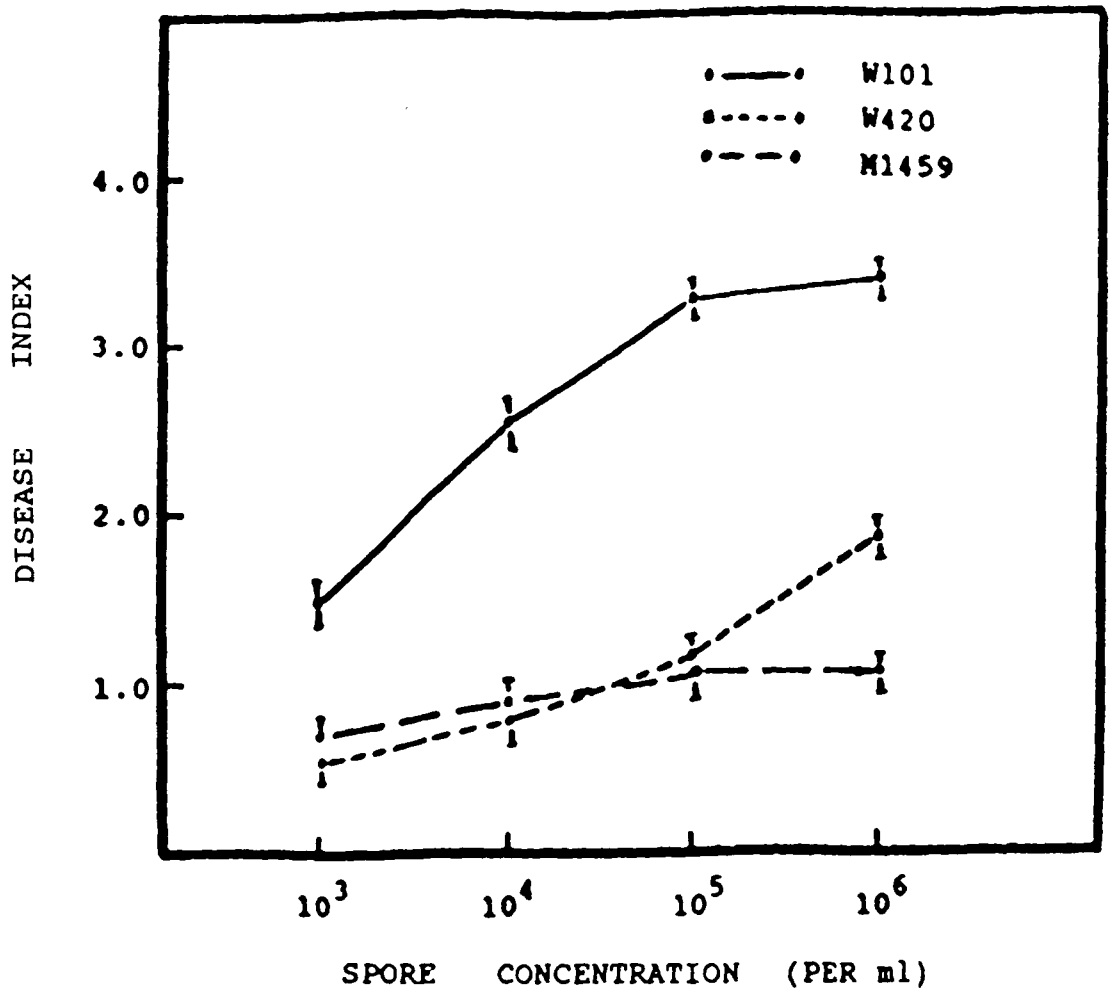

Figure 5. Effect of the spore concentration of Botrytis allii on disease index of the second scale layer of three onion inbred lines, vertical bars show the SE for each mean.

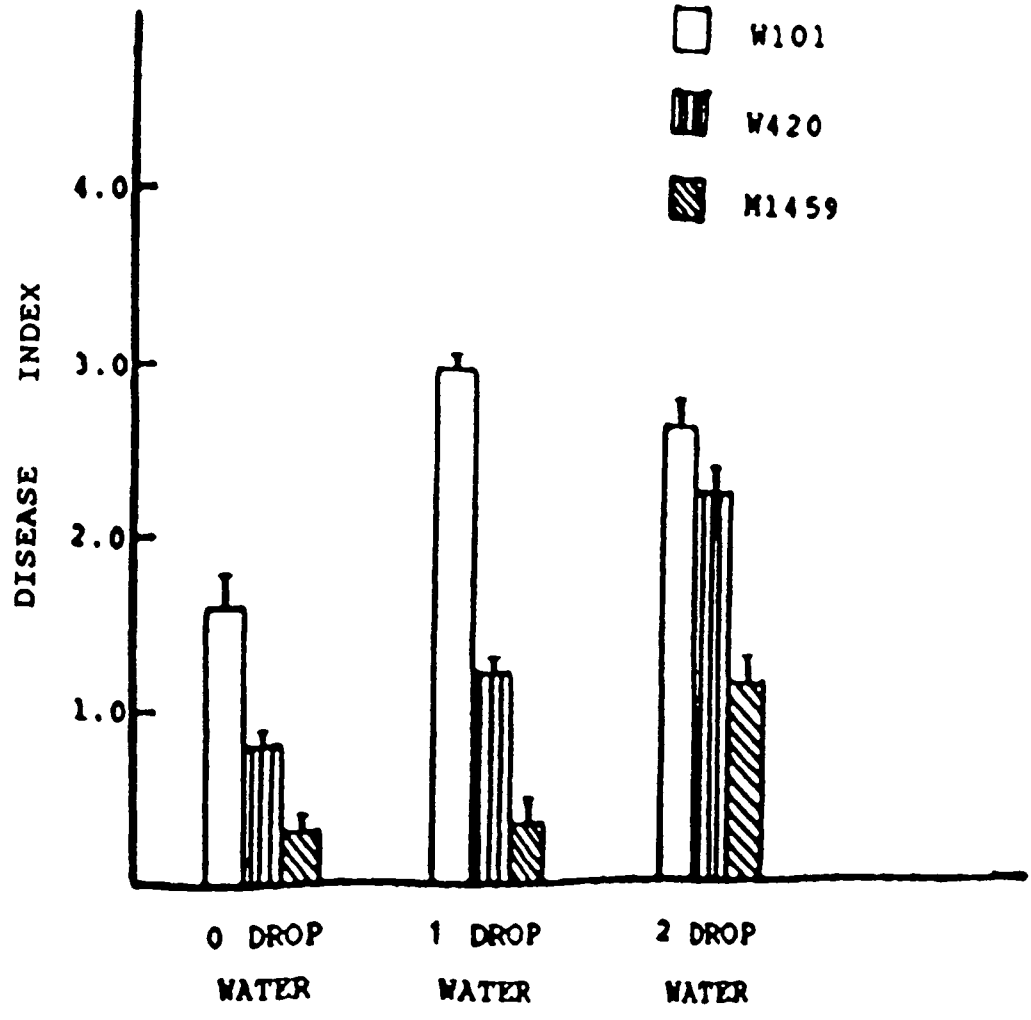

Figure 6. Effect of the number of drops of distilled water added to the spore suspension of Botrytis allii on the neck-rot disease index of the second scale layer of three onion inbred lines, vertical bars show the SE for each mean.

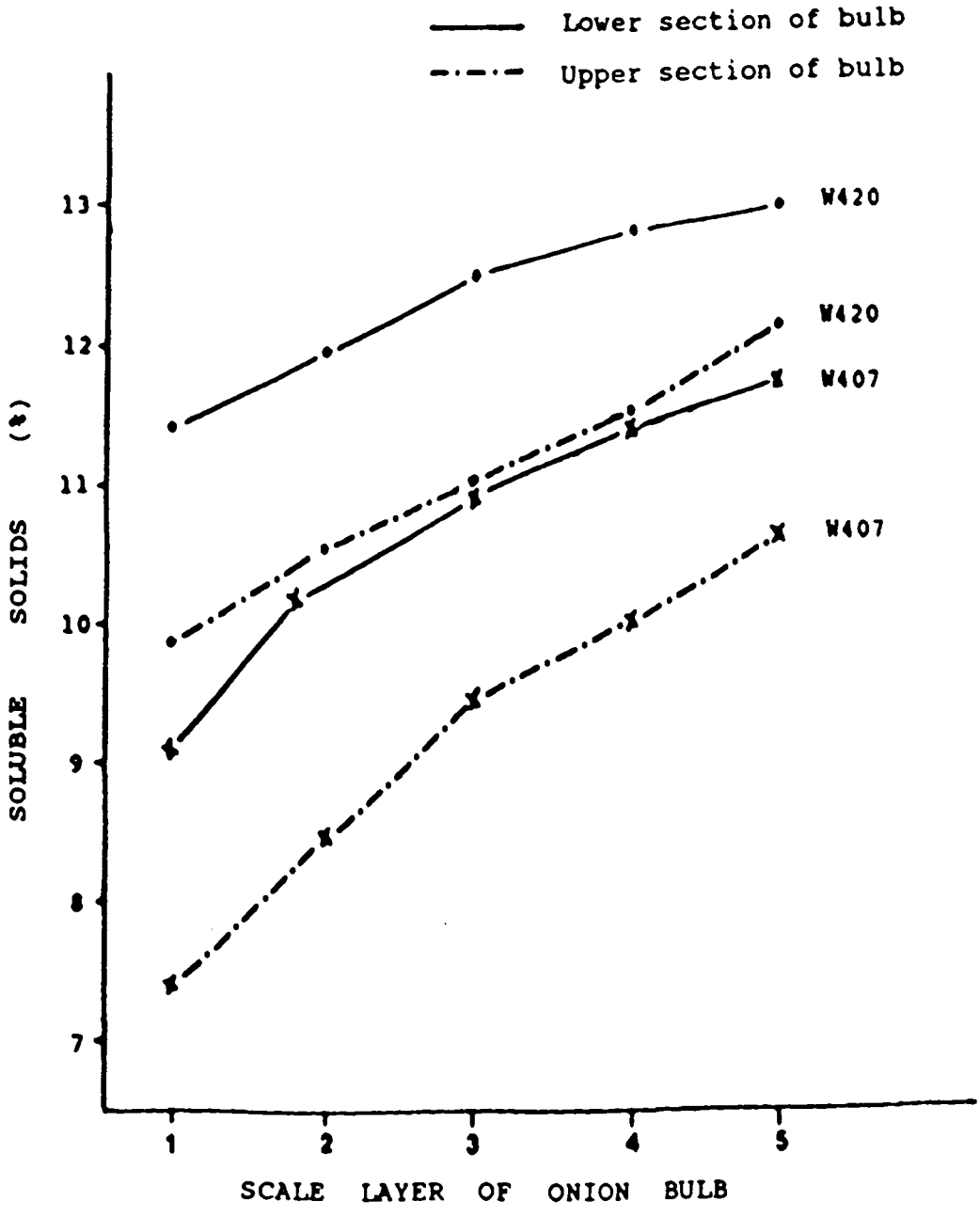

Figure 7. The soluble solids content of onion bulb scale tissue from the outer (layer 1) to inner (layer 5) and of upper and lower bulb sections in two inbred lines.

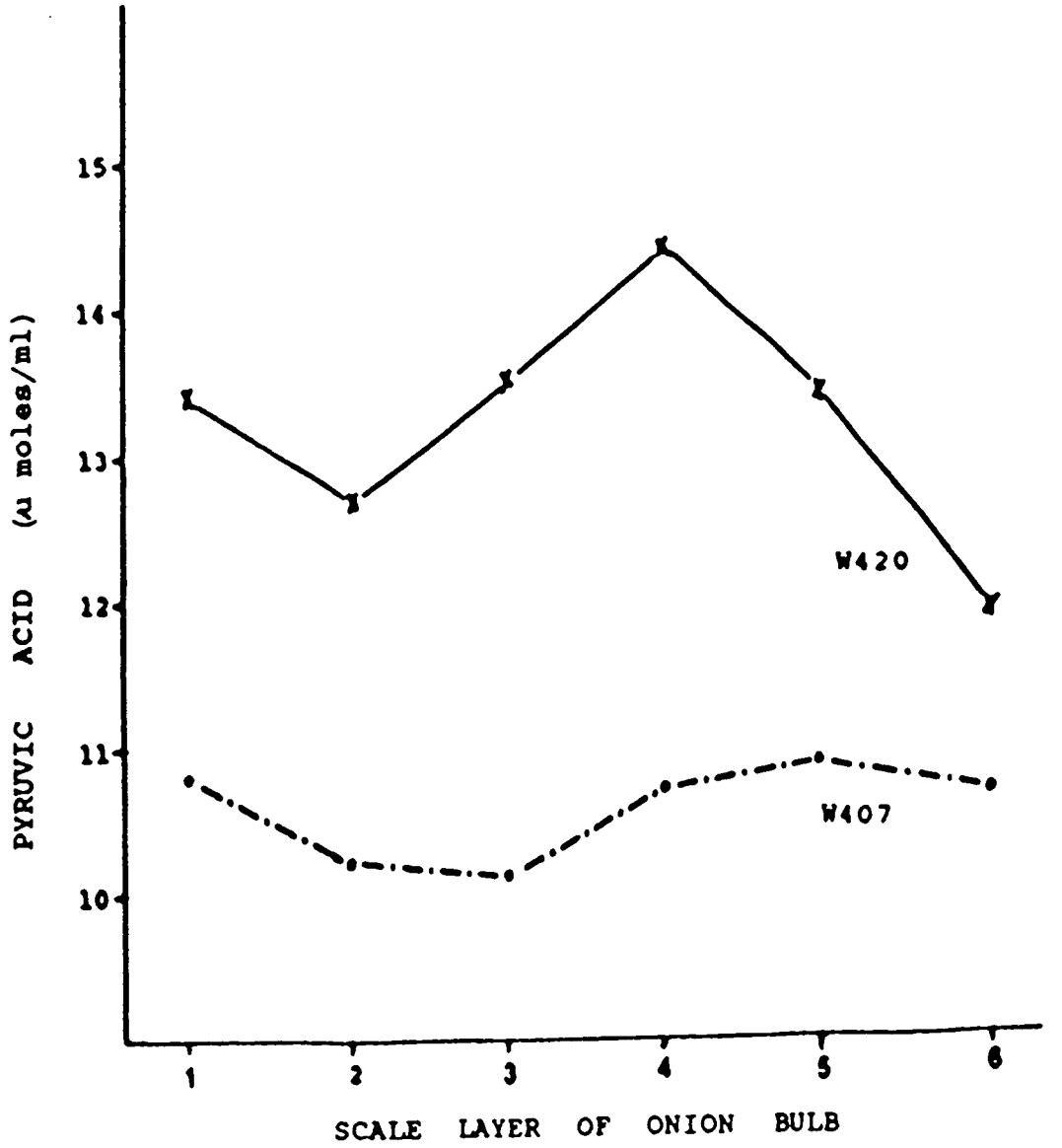

Figure 8. The pyruvic acid concentration of onion bulb scale tissue from the outer (layer 1) to inner (layer 6) layer of two inbred lines.

ANALYSES OF DIALLEL CROSS

Means of the parental lines and their F_1 progenies are presented in Tables 3, 4, 5, for DI, PA, and SS, respectively. Each of the nine F_1 progeny mean DI values were lower than the mean DI of their respective common parents (Table 3). The mean DI values for the progenies of W407, W202 and Ial63 were each significantly below their common parent mean at the 0.01 level. This indicates that the F_1 progenies exhibited more resistance to neck-rot than did their parents. Twenty seven of the 36 F_1 hybrids had lower DI values than their more resistant parent.

The F_1 progeny mean PA concentrations of the four most pungent parents were all significantly lower than their parental values (Table 4). Twenty seven of the 36 F_1 hybrids had lower PA values than their more pungent parent.

Three F_1 progenies had mean SS values significantly below their common parent (Table 5). However, only three F_1 hybrids had SS values that fell outside the range of their parental values.

Heterosis effect of Neck-rot disease index, pyruvic acid and soluble solids

The heterosis effect of DI, PA, and SS was calculated for each F_1 hybrid as percent deviation from their respective mid-parent values (Tables 6-8). There was a strong pattern of heterosis for resistance (lower DI values) among the the F_1 hybrids (Table 6). Fifteen of the 36

hybrids had DI values significantly lower than their respective midparent values. No hybrid had a significantly higher DI than its midparent value. Most of the heterotic crosses involved at least one of the three most resistant parents (W420, B6693 and M5718). Four of the eight crosses involving W420, five crosses involving B6693 and six crosses involving M5718 were significantly heterotic for resistance. In contrast, no hybrid having P6502 as a parent was heterotic for resistance.

F_1 hybrids tended to be less pungent than their mid-parent values (Table 7). Thirteen crosses were significant in negative heterosis for PA. Six of the eight crosses involving B6693 were significantly below their midparent value for PA.

Mid-parent deviations for SS in the hybrids ranged from -7.1% to 4.9% (Table 8), indicating that most of the F_1 hybrids were close to their parental means. Thirty five F_1 hybrids did not differ significantly from their mid-parent values.

Analysis of combining ability

The general combining ability (GCA) mean squares were highly significant for DI, PA, and SS (Table 13). Specific combining ability (SCA) mean squares of the three traits were significant at 0.05 level. The GCA mean squares were much larger than the corresponding SCA mean squares and

Table 3. Mean neck-rot disease index of onion parental lines and their F_1 diallel progeny.

	B6693	M5718	M8155	PG1b	P6502	W407	W202	D420	Ia163
B6693	2.06	----	----	----	----	----	----	----	----
M5718	0.66	2.10	----	----	----	----	----	----	----
M8155	1.06	1.89	2.37	----	----	----	----	----	----
PG1b	1.80	1.95	2.34	2.99	----	----	----	----	----
P6502	1.94	2.09	2.65	2.70	2.80	----	----	----	----
W407	1.73	1.80	2.60	2.98	3.12	3.50	----	----	----
W202	1.69	1.70	2.21	3.23	2.75	3.08	3.43	----	----
W420	1.48	1.15	1.20	1.50	1.82	2.11	2.18	1.92	----
Ia163	2.04	2.27	2.21	3.00	2.83	3.18	3.15	2.77	3.60
Mean[z]	1.61	1.73	2.06	2.50	2.52	2.68**	2.60**	1.79	2.78**
$LSD_{.05}$	0.57	0.63	0.78	0.82	0.66	0.54	0.51	0.72	0.75

*, ** Mean of F_1 progeny significantly below the common parent at 0.05 and 0.01 level, respectively.

[z] Mean = F_1 progeny mean.

Table 4. Mean pyruvic acid concentration (μ moles/g) of onion parental lines and their F_1 diallel progeny.

	B6693	M5718	M8155	PG1b	P6502	W407	W202	W420	Ia163
B6693	14.1	----	----	----	----	----	----	----	----
M5718	11.1	11.9	----	----	----	----	----	----	----
M8155	9.6	10.2	10.2	----	----	----	----	----	----
PG1b	10.6	10.1	8.6	9.5	----	----	----	----	----
P6502	9.0	8.9	7.5	8.5	8.6	----	----	----	----
W407	11.2	11.5	9.5	10.0	8.0	10.2	----	----	----
W202	11.0	12.0	9.8	10.3	8.7	11.2	12.2	----	----
W420	10.9	12.0	11.0	11.4	9.7	11.0	11.5	12.8	----
Ia163	10.7	10.3	10.5	10.0	8.5	11.2	10.7	10.9	10.1
Mean[z]	10.5**	10.7*	9.6	9.9	8.6	10.4	10.7**	11.0**	10.3
$LSD_{.05}$	0.7	1.3	1.5	1.2	0.8	1.4	1.5	1.6	1.3

*,** Mean of F_1 progeny significantly below the common parent at 0.05 and 0.01 level, respectively.

[z] Mean = F_1 progeny mean.

Table 5. Mean soluble solids content (%) of onion parental lines and their F_1 diallel progeny.

	B6693	M5718	M8155	PG1b	P6502	W407	W202	W420	Ia163
B6693	11.2	----	----	----	----	----	----	----	----
M5718	10.3	10.2	----	----	----	----	----	----	----
M8155	10.8	9.5	9.6	----	----	----	----	----	----
PG1b	9.1	9.2	8.5	8.0	----	----	----	----	----
P6502	8.9	9.1	8.4	7.6	8.0	----	----	----	----
W407	9.5	9.5	9.6	8.1	7.7	8.6	----	----	----
W202	9.8	9.4	9.4	8.3	8.0	8.7	8.7	----	----
W420	10.3	10.2	9.8	9.0	9.2	9.4	9.2	10.3	----
Ia163	10.2	9.4	9.5	8.6	8.1	9.1	8.6	9.4	8.8
Mean[z]	9.9**	9.6**	9.4	8.5	8.4	8.9	8.9	9.6*	9.1
$LSD_{.05}$	0.5	0.6	0.6	0.7	0.8	0.6	0.7	0.7	0.6

*,** Mean of F_1 progeny significantly below the common parent at 0.05 and 0.01 level, respectively.

[z] Mean = F_1 progeny mean.

Table 6. Heterosis[z] (%) of neck-rot disease index of onion F_1 diallel progeny.

	M5718	M8155	PG1b	P6502	W407	W202	W420	Ia163
B6693	-68.2**	-52.0*	-27.1	-20.1	-37.7**	-38.3**	-25.6	-27.9**
M5718	---	-15.2	-23.2*	-14.6	-35.7**	-38.4**	-42.7**	-20.3*
M8155	---	---	-12.6	2.7	-11.5	-23.7*	-43.9**	-25.8*
PG1b	---	---	---	-6.5	-8.0	0.6	-38.7**	-8.8
P6502	---	---	---	---	-0.9	-11.5	-22.8	-11.5
W407	---	---	---	---	---	-10.9	-22.1*	-10.4
W202	---	---	---	---	---	---	-18.3	-10.2
W420	---	---	---	---	---	---	---	0.3

*, ** F_1 mean differs significantly from mid-parent value at 0.05 and 0.01 level, respectively.

[z] Heterosis = (F_1 - mid-parent / mid-parent) x 100.

Table 7. Heterosis[z] (%) of pyruvic acid concentration of onion F_1 diallel progeny.

	M5718	M8155	PG1b	P6502	W407	W202	W420	Ia163
B6693	-14.5**	-20.8**	-9.6	-20.7**	-7.9	-16.2**	-18.8**	-11.8**
M5718	----	-8.1	-5.4	-12.9*	3.8	-0.5	-3.3	-6.9
M8155	----	----	-12.4*	-20.5**	-7.3	-12.2*	-4.2	2.7
PG1b	----	----	----	-6.4	1.3	-4.7	2.2	2.0
P6502	----	----	----	----	-14.8**	-15.5**	-9.4*	-8.9
W407	----	----	----	----	----	0.4	-4.5	9.5
W202	----	----	----	----	----	----	-7.5	3.6
W420	----	----	----	----	----	----	----	-4.7

*, ** F_1 mean differs significantly from mid-parent value at 0.05 and 0.01 level, respectively.

[z] Heterosis = (F_1 - mid-parent / mid-parent) x 100.

Table 8. Heterosis[z] (%) of soluble solids content of onion F_1 diallel progeny.

	M5718	M8155	PG1b	P6502	W407	W202	W420	Ia163
B6693	-2.6	4.2	-4.9	-7.1*	-4.0	-2.0	-4.0	2.2
M5718	---	3.7	1.5	1.2	2.1	-0.2	-0.2	-0.4
M8155	---	---	-3.8	-3.7	4.9	2.4	-1.5	3.2
PG1b	---	---	---	-5.3	-2.6	-1.2	-2.0	2.1
P6502	---	---	---	---	-7.5	-4.2	0.4	-3.2
W407	---	---	---	---	---	-0.3	-0.8	4.5
W202	---	---	---	---	---	---	-3.2	-1.8
W420	---	---	---	---	---	---	---	-1.2

*, ** F_1 mean differs significantly from mid-parent value at 0.05 and 0.01 level, respectively.

[z] Heterosis = (F_1 - mid-parent / mid-parent) x 100.

highly significant for all three traits. This indicates that additive gene effects of these parents were more important than nonadditive effects in determining performance of the F_1 hybrids.

The observed means of DI, PA, and SS of nine parents, their general combining ability (GCA) effects, and the variances of specific combining ability (SCA) effects are presented in Tables 9-11. The three most resistant lines B6693, M5718 and W420 had low DI, but high PA and SS means. These lines also had the largest negative GCA effects for DI and the largest positive GCA effects for SS, reflecting their transmission of high solids and high resistance to their progeny. While resistant lines M5718 and W420 also had large positive GCA effects for PA, resistant line B6693, which had the highest mean PA, had only moderately positive GCA effects for PA, lower than the GCA effects for PA of susceptible line W202.

Lines W407, W202 and Ia163 were the three most neck-rot susceptible lines as indicated by their high mean DI values (Table 9). These parents also had the highest GCA effects for DI indicating that their susceptibility was transmitted to their hybrids. All of these lines, however, had moderate to high PA means and moderate to high GCA effects for PA (Table 10). W202 had the third highest GCA effect for PA. Thus, in this study the most susceptible lines were not the least pungent lines.

Line P6502 had the lowest mean PA (8.6) and the largest negative GCA effect (-1.84) for PA, indicating that this yellow sweet Spanish type line was the least pungent of the study and tended to produce the least pungent hybrids. The other yellow sweet Spanish line in this study, PG1b, had the second lowest mean PA (9.5) which did not differ siginifcantly from P6502. However, its GCA effect for PA (-.30), although negative, was much smaller than the GCA effect for PA of line P6502. The yellow globe line M8155 had a larger negative GCA effect for PA (-.72) than did PG1b. P6502, Pg1b and M8155 all had intermediate DI mean values (Table 9), with M8155 being the most resistant of the group. Their GCA effects for DI indicate a somewhat greater range in their breeding value for DI. M8155 had a GCA effect for DI of -.19 and P6502 had a GCA effect of .34.

The low variances of SCA effects for DI associated with W407, P6502, and W202 suggests that they uniformly transmitted their high DI to all of their F_1 hybrids. Line W420 had the highest variances of SCA effects for DI and PA, reflecting the greater variation for these traits among crosses involving this parent. The low variances of SCA effects for DI and PA associated with B6693 indicates that it more uniformly transmitted its performance to its F_1 hybrids.

Table 9. Means, estimates of general combining ability (g_i) , and variances of specific combining ability (S^2_{si}) of neck-rot disease index of nine onion inbred lines used as parents in a diallel cross.

Parents	Disease index		
	Mean	g_i	S^2_{si}
B6693	2.0 e[y]	-0.73	0.055
M5718	2.1 e	-0.57	0.054
M8155	2.3 de	-0.19	0.088
PG1b	2.9 bc	0.28	0.060
P6502	2.8 cd	0.34	0.041
W407	3.5 a	0.44	0.015
W202	3.4 ab	0.35	0.041
W420	1.9 e	-0.47	0.126
Ia163	3.6 a	0.56	0.061
Mean	2.75		
$LSD_{.05}$	0.45		

[y] Means within columns followed by the same letter are not significantly different at 0.05 level, Duncan's multiple range test.

Table 10. Means, estimates of general combining ability (g_i), and variances of specific combining ability (S^2_{si}) of pyruvic acid concentration of nine onion inbred lines used as parents in a diallel cross.

Parents	Pyruvic acid concentration (u moles/g.) Mean	g_i	S^2_{si}
B6693	14.1 a[y]	0.34	0.067
M5718	11.9 b	0.62	0.144
M8155	10.2 c	-0.72	0.172
PG1b	9.5 cd	-0.30	0.121
P6502	8.6 d	-1.84	0.096
W407	10.2 c	0.27	0.110
W202	12.2 b	0.52	0.157
W420	12.8 b	0.97	0.197
Ia163	10.1 cd	0.15	0.131
Mean	11.04		
$LSD_{.05}$	1.06		

[y] Means within columns followed by the same letter are not significantly different at 0.05 level, Duncan's multiple range test.

Table 11. Means, estimates of general combining ability (g_i), and variances of specific combining ability (S^2_{si}) of percent soluble solids of nine onion inbred lines used as parents in a diallel cross.

	Percent soluble solids		
Parents	Mean	g_i	S^2_{si}
B6693	11.2 a[y]	0.82	0.071
M5718	10.1 b	0.48	0.075
M8155	9.6 bc	0.33	0.113
PG1b	8.0 d	-0.70	0.032
P6502	8.0 d	-0.89	0.077
W407	8.6 cd	-0.23	0.051
W202	8.7 cd	-0.26	0.016
W420	10.3 ab	0.47	0.039
Ia163	8.8 cd	-0.02	0.040
Mean	9.30		
$LSD_{.05}$	0.93		

[y] Means within columns followed by the same letter are not significantly different at 0.05 level, Duncan's multiple range test.

Table 12. Means and estimates of specific combining ability effects (S_{ij}) of pyruvic acid concentration (µ moles/g), percent soluble solids and neck-rot disease index of onion F_1 diallel progeny.

	Pyruvic acid		Soluble solids		Disease index	
Crosses	Mean	s_{ij}	Mean	s_{ij}	Mean	s_{ij}
B6693xM5718	11.14	-0.07	10.37	-0.12	0.66	-0.23
B6693xM8155	9.65	-0.08	10.87	0.53	1.06	-0.21
B6693xPG1b	10.69	0.40	9.15	-0.16	1.80	0.06
B6693xP6502	9.01	0.27	8.91	-0.21	1.94	0.14
B6693xW407	11.22	0.36	9.54	-0.23	1.73	-0.17
B6693xW202	11.01	-0.10	9.80	0.06	1.69	-0.12
B6693xW420	10.97	-0.59	10.34	-0.14	1.48	0.49
B6693xIa163	10.70	-0.04	10.26	0.27	2.04	0.02
M5718xM8155	10.21	0.06	9.50	-0.50	1.89	0.47
M5718xPG1b	10.17	-0.40	9.22	0.25	1.95	0.05
M5718xP6502	8.97	-0.06	9.16	0.38	2.09	0.13
M5718xW407	11.55	0.41	9.58	0.14	1.80	-0.17
M5718xW202	12.02	0.63	9.42	0.01	1.70	-0.27
M5718xW420	12.00	0.16	10.20	0.06	1.15	0.00
M5718xIa163	10.31	-0.71	9.44	-0.21	2.27	0.09
M8155xPG1b	8.68	-0.55	8.51	-0.31	2.34	0.06
M8155xP6502	7.51	-0.18	8.49	-0.14	2.65	0.31
M8155xW407	9.52	-0.28	9.61	0.32	2.60	0.16
M8155xW202	9.85	-0.20	9.44	0.19	2.21	-0.14
M8155xD420	11.07	0.57	9.85	0.14	1.20	-0.32
M8155xIa163	10.50	0.82	9.56	0.06	2.21	-0.35
PG1bxP6502	8.50	0.39	7.60	0.00	2.70	-0.11
PG1bxW407	10.04	-0.18	8.14	-0.11	2.98	0.07
PG1bxW202	10.35	-0.12	8.33	0.11	3.23	0.40
PG1bxW420	11.45	0.53	9.02	0.06	1.50	-0.50
PG1bxIa163	10.06	-0.04	8.64	0.17	3.00	-0.04
P6502xW407	8.05	-0.62	7.70	-0.36	3.12	0.15
P6502xW202	8.79	-0.14	8.03	0.00	2.75	-0.13
P6502xW420	9.72	0.35	9.22	0.45	1.82	-0.24
P6502xIa163	8.56	0.01	8.16	-0.12	2.83	-0.26
W407xW202	11.28	0.24	8.70	0.01	3.08	0.10
W407xW420	11.03	-0.46	9.43	0.003	2.11	-0.05
W407xIa160	11.20	0.53	9.17	0.23	3.18	-0.01
W202xW420	11.59	-0.15	9.26	-0.13	2.18	0.11
W202xIa163	10.78	-0.14	8.67	-0.24	3.15	0.04
W420xIa163	10.97	-0.40	9.49	-0.15	2.77	0.49

Table 13. Combining ability mean squares for pyruvic acid, soluble solids and neck-rot disease index of onion diallel cross.

Source	DF	Pyruvic acid	Soluble solids	Disease index
G. C. A.[z]	8	5.17**	2.31**	1.71**
S. C. A.[y]	27	0.19*	0.07*	0.07*
G.C.A./S.C.A.		26.6	33.5	22.7

** = Significant at 1% level, * = at 5 % level.

[z] G.C.A.= general combining ability.
[y] S.C.A.= specific combining ability.

Correlations among traits

The correlation coefficients calculated from F_1 progeny data among the three traits were all highly significant (Table 14). PA content of the hybrids had a moderate positive correlation with SS (r = 0.57), indicating that the more pungent hybrids tended to have higher soluble solids concentrations. SS content of the hybrids had a moderate negative correlation with DI of about the same magnitude as PA with SS (r= -0.63). This indicates that the hybrids with higher soluble solids concentrations tended to be more resistant to neck-rot. PA content of the hybrids had a smaller, but significant, negative correlation with DI (r = - 0.35). While this statistic indicates a significant association between neck-rot resistance and higher pungency in this material, its relatively small magnitude also reflects the performance of hybrids that had relatively low DI and low PA such as B6693 X M8155, and hybrids that had relatively high DI and high PA such as W407 X Ia160 (Table 12).

Table 14. Phenotypic correlation coefficients of pungency (pyruvic acid), soluble solids and neck-rot disease index calculated from onion diallel cross.

	Soluble Solids	Pungency
Pungency	0.57**	-----
Neck-rot disease index	-0.63**	-0.35**

** Significant at 1 % level.

ANALYSIS OF GENERATIONS

Four onion crosses, W420 x Pg-1b , W202 x D10-1b, W420 x D10-1b and B6693 x Pg-1b, involved high SS, neck-rot resistant parents crossed with low SS, neck-rot susceptible parents. Cross W420 x B6693 involved a cross with two medium SS, neck-rot resistant parents. Cross W407 x D10-1b involved two low SS, neck-rot susceptible parents crossed together. Cross W420 x Pg-1b was selected as being typical of the most informative cross category for a more detailed presentation of results.

In addition to the frequency distributions shown graphically for W420 x Pg-1b (Figs. 9-11) and for all crosses in Tables 15-20, generation means are shown in Table 21, and graphically in Figs. 12-14. In these graphs, the parents and progeny populations are represented on the horizontal axis, and mean value of DI, PA, and SS are represented on the vertical axis. If the mode of inheritance is additive, the graph will show a straight line, with F_1 and F_2 intermediate between P_1 and P_2, BC_1 intermediate between P_1 and F_1, and BC_2 intermediate between P_2 and F_1. Any deviation from a straight line is an indication of dominance of one parent or in some situations, heterosis.

Frequency distributions of individuals for DI, PA, and SS in parental and progeny populations are expressed in two

ways for the cross W420 x Pg-1b (Figs. 9-11 and Table 15).

Neck-rot resistance

Distributions of P_1 and P_2 plants for DI overlapped slightly, but the predominate classes of the two parents were distinct (Fig. 9). The overlap was primarily in score class 2. The DI distribution of the F_1 was skewed strongly toward the susceptible parent (P_2), but extended over the entire scoring range. The percentage of the predominant class was 62.9 % for P_2 compared to 38 % for the F_1 (Table 15).

The distributions of backcross plants for DI tended to be broad and flat but were skewed slightly toward their respective parents. Thus, BC_1 had a complete absence of score 4 plants and BC_2 had very few (4.4%) in the resistant class with most plants falling in the 2, 3, and 4 score categories. The F_2 distribution covered the range but, similar to the F_1, was skewed moderately toward the susceptible category.

Frequency distributions for DI generally indicated quantitative additive inheritance with some dominance of susceptibility. Population means (Table 21, Fig. 12) generally support additive inheritance of DI in this cross.

Graphed generation means for DI (Fig. 12) follow a straight line (additive) relationship except for the F_1. The deviation of the F_1 from the mid-parent value was non-

significant (Table 27). Although the deviation of BC_1 from its respective mid-parent value was significant, its position on Fig. 12 closely supported additive inheritance.

Soluble solids content

The parental frequency distributions for SS did not overlap (Fig. 10). The F_1 distribution was slightly skewed toward the high solids parent. BC_1 was strongly skewed toward P_1, and BC_2 less strongly skewed toward P_2. The F_1, BC_1, and BC_2 distributions for soluble solids agree with the slight dominance shown by the means of these generations (Fig. 13). The deviations of the F_1 and BC_2 means from their mid-parent values were non-significant, but that of BC_2 was significant (Table 29). The F_2 frequency distribution (Fig. 10) was symmetrical and suggestive of additive inheritance; and the position of the F_2 mean (Fig. 13) indicated additive inheritance.

Pyruvic acid content

The frequency distributions of P_1 and P_2 for PA overlapped slightly (Fig. 11). The distribution of the F_1 covered the same range as P_1 and was similar in configuration. The F_2 distribution did not cover the entire range of distribution found in the parents and was close to symmetrical.

The backcrosses resembled their respective parent lines in both range and position of their distributions, except that BC_1 had a higher percentage of plants in the 12-16 u moles/g range. This is also apparent in the generation means (Fig. 14, Table 21). The deviation of BC_1 from its mid-parent value was significant at 1 % probability (Table 28). Except for this relationship between BC_1 and P_1, additive inheritance is generally suggested by the data. The lower level PA in the F_1 than in the F_2 suggests that heterosis for vigor and bulb size may have reduced PA content.

Table 15. Frequency distribution (percentage) for neck-rot disease index, pyruvic acid, and soluble solids content in a cross between W420 (P_1) x PG-1b (P_2).

	Neck-rot disease index				
	0	1	2	3	4
P_1	50.0	42.2	6.2	1.6	
P_2			11.1	25.9	62.9
F_1	2.0	14.0	12.0	32.0	38.0
BC_1	35.9	29.6	14.0	20.3	
BC_2	4.4	8.8	31.1	26.6	28.8
F_2	11.2	16.3	23.4	26.5	32.6

	Pyruvic acid (u moles/g)					
	6	8	10	12	14	16
P_1			28.1	32.8	34.3	4.6
P_2	33.3	53.7	12.9			
F_1		20.4	59.1	20.1		
BC_1			6.2	42.2	40.6	10.9
BC_2	13.3	42.2	37.7	6.6		
F_2	4.0	12.2	50.0	20.4	12.2	

	Soluble solids content (%)							
	6	7	8	9	10	11	12	13
P_1				1.5	12.5	42.2	37.5	6.2
P_2	25.9	61.1	12.9					
F_1			12.2	26.5	44.8	16.3		
BC_1					9.4	37.5	42.2	10.9
BC_2	2.2	26.6	24.4	31.1	13.3	2.2		
F_2		9.1	23.4	29.6	25.5	9.1	3.1	

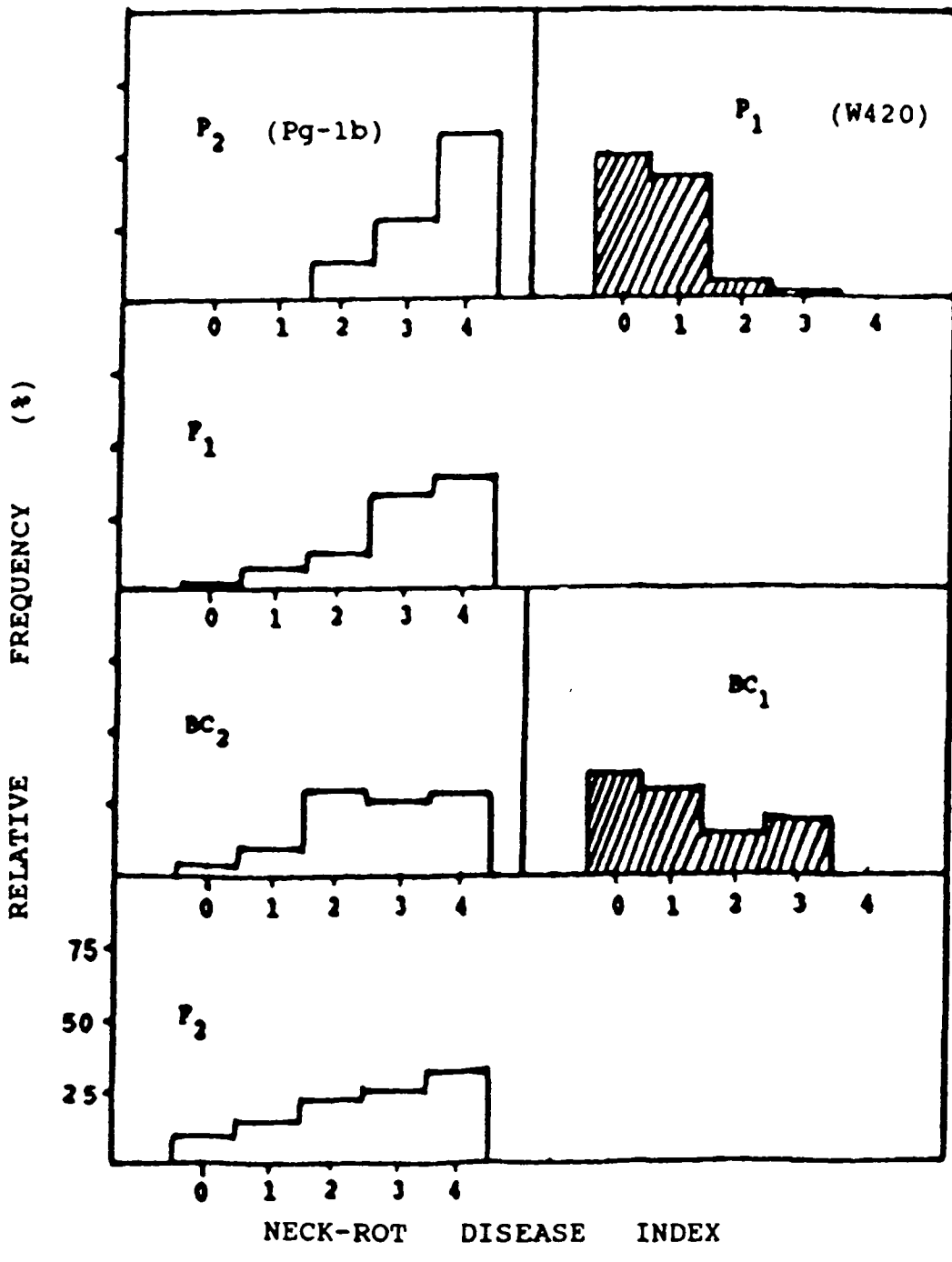

Figure 9. Frequency distribution of neck-rot disease index of the parents and progenies of W420 x Pg-1b.

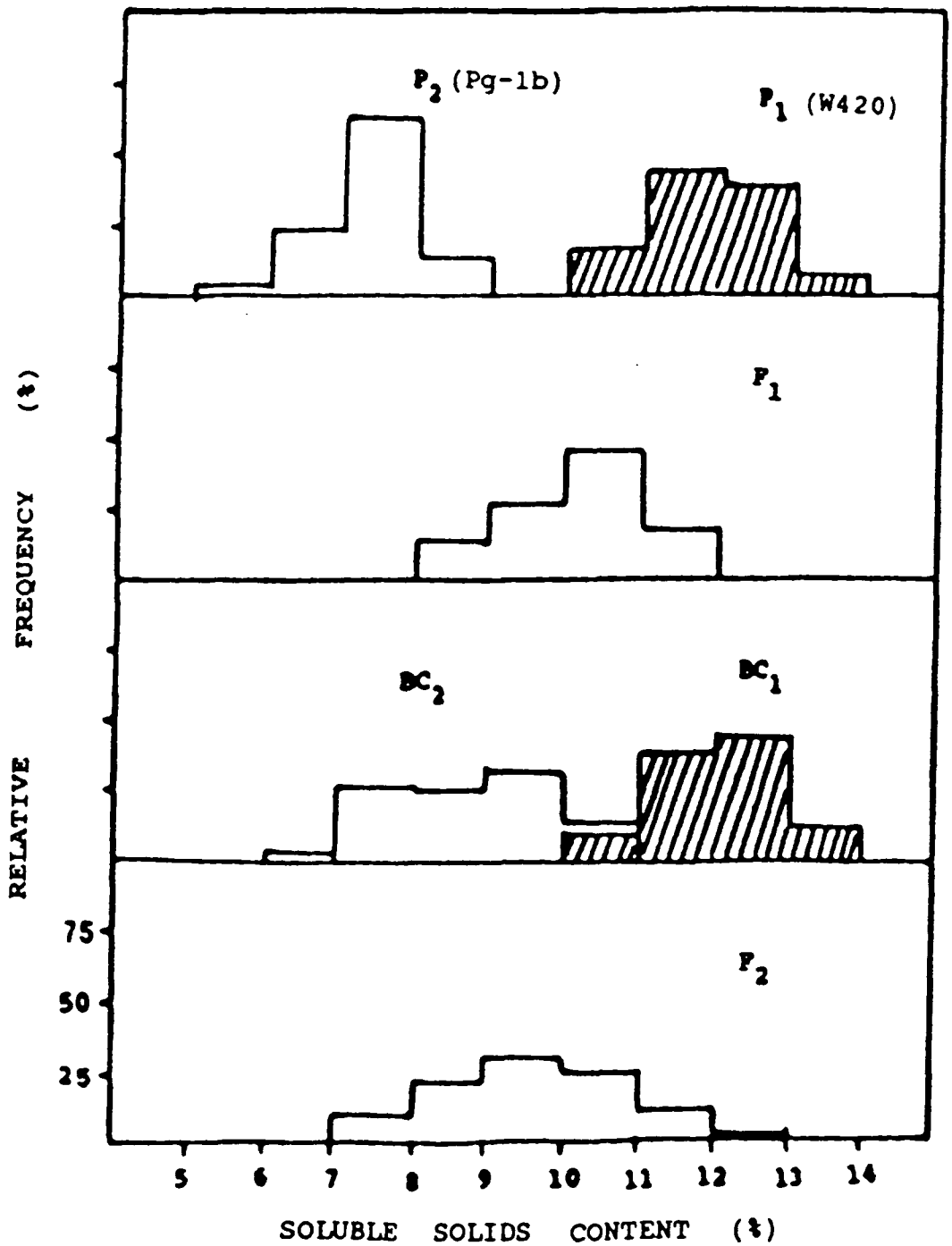

Figure 10. Frequency distribution of percent soluble solids content of the parents and progenies of W420 x Pg-1b.

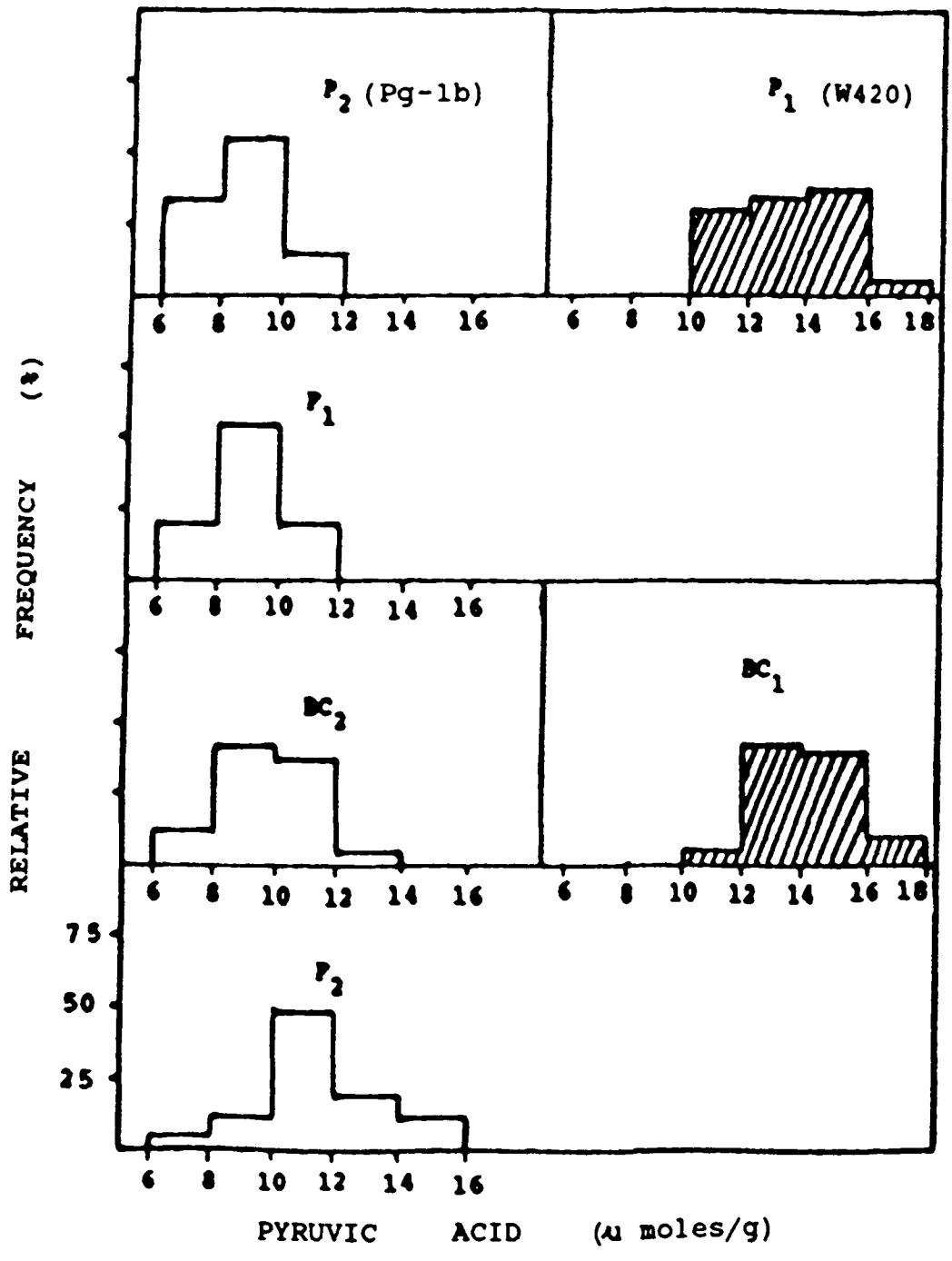

Figure 11. Frequency distribution of pyruvic acid concentration of the parents and progenies of W420 x Pg-1b.

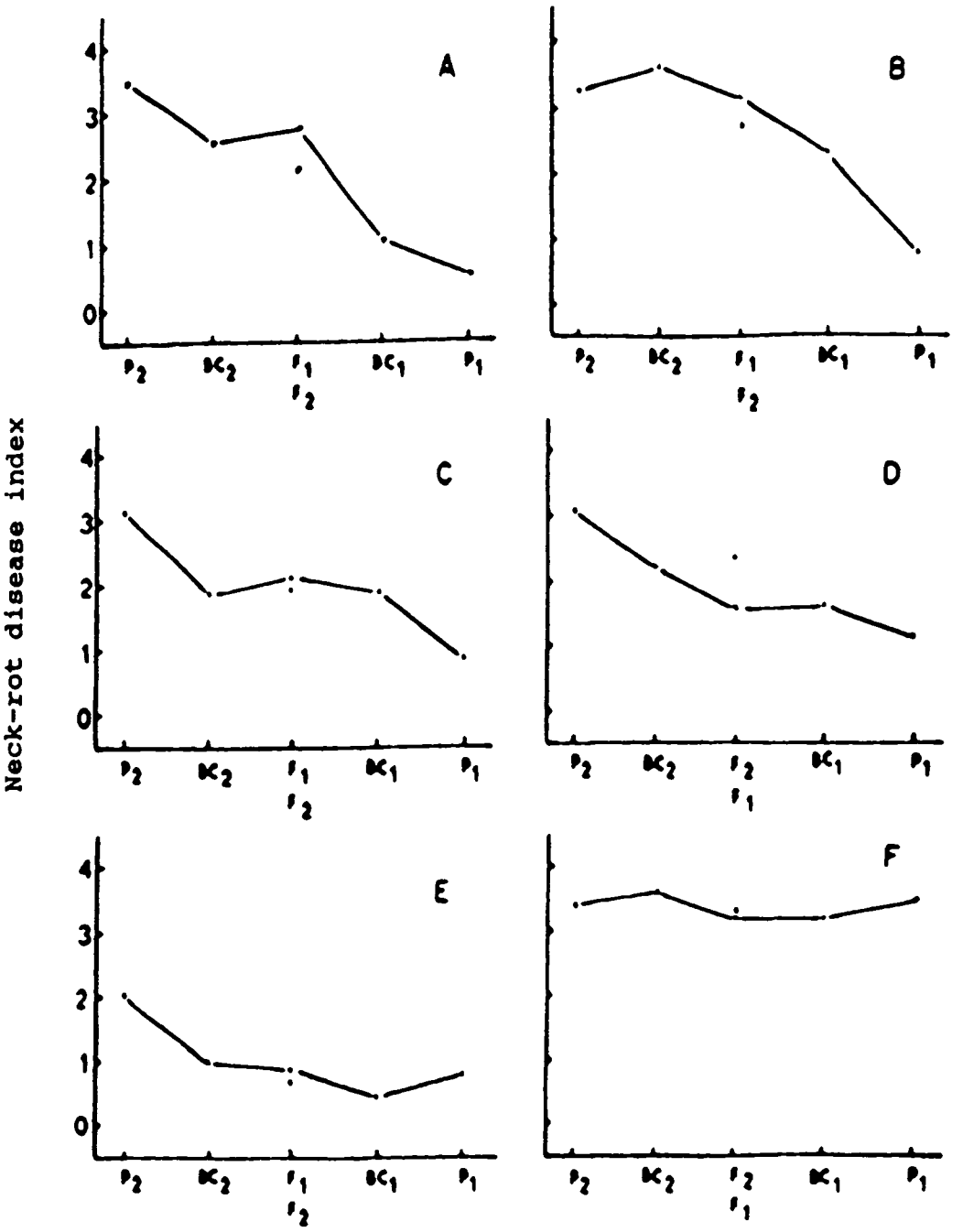

Figure 12. Generation means of neck-rot disease index of parents and progenies in onion crosses: A) W420 x Pg-1b, B) W202 x D10-1b, C) W420 x D10-1b, D) B6693 x Pg-1b, E) W420 x B6693, F) W407 x D10-1b.

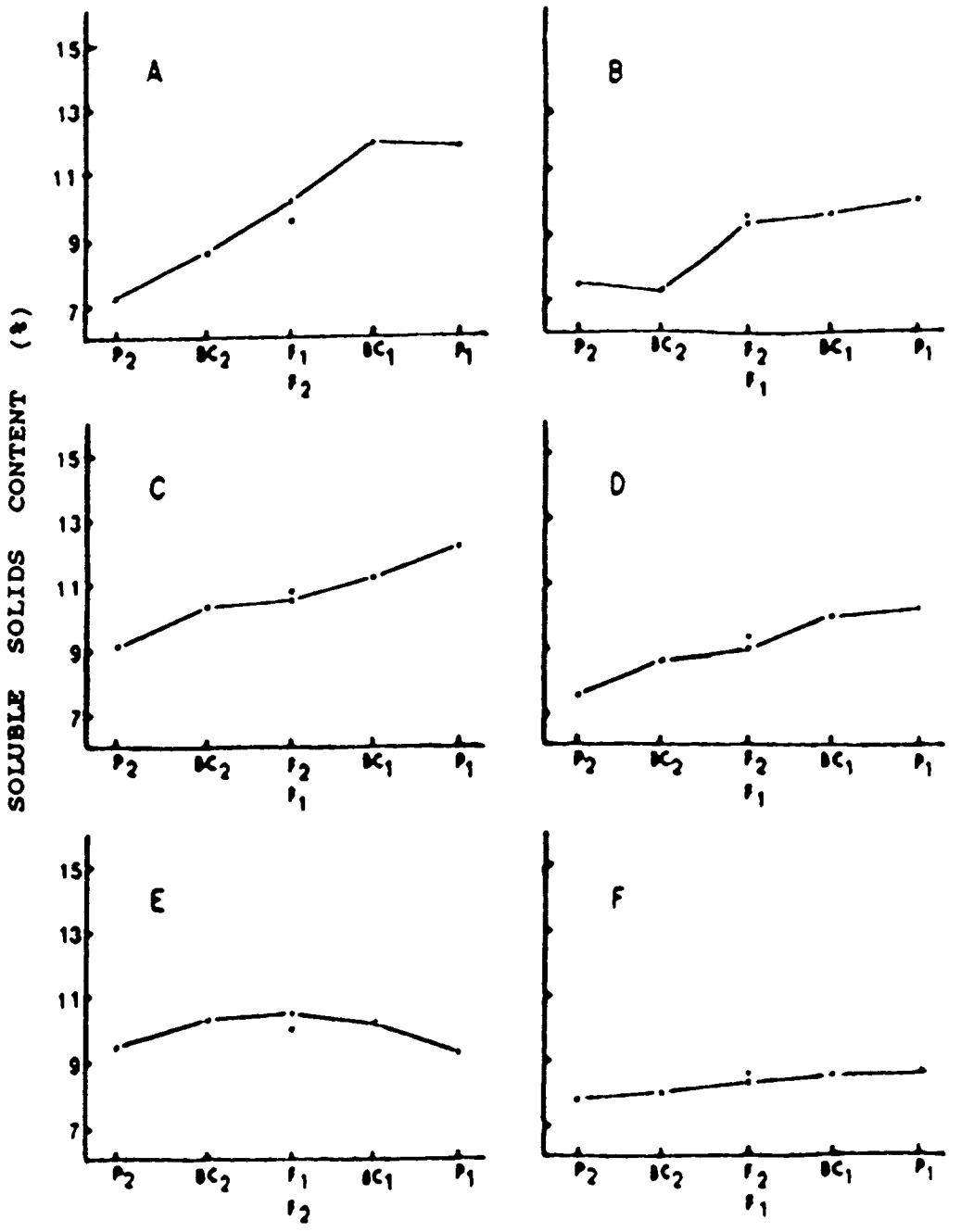

Figure 13. Generation means of soluble solids content of parents and progenies in onion crosses: A) W420 x Pg-1b, B) W202 x D10-1b, C) W420 x D10-1b, D) B6693 x Pg-1b, E) W420 x B6693, F) W407 x D10-1b.

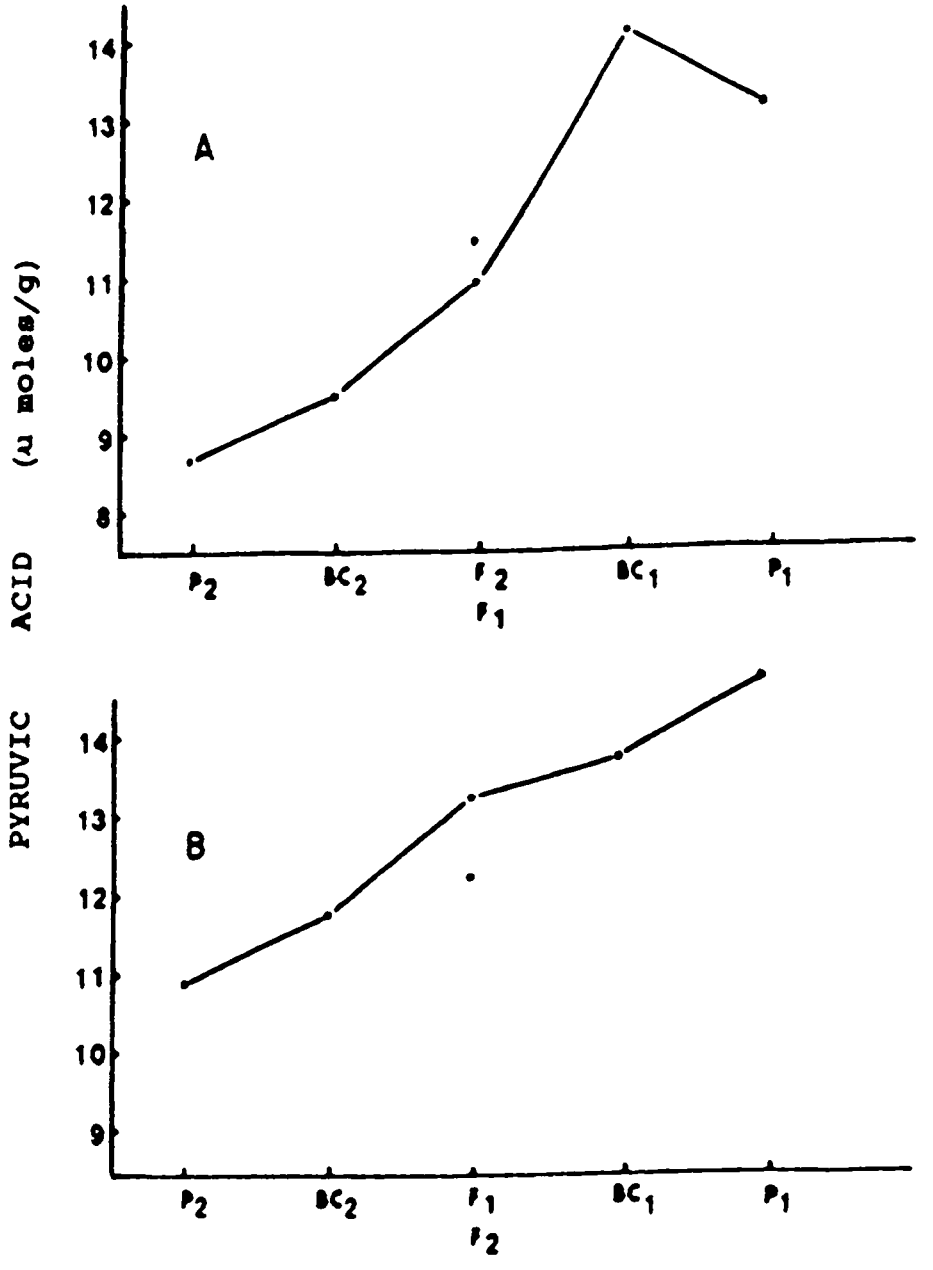

Figure 14. Generation means of pyruvic acid content of parents and progenies in onion crosses: A) W420 x Pg-1b, B) W420 x B6693.

Additional crosses

The frequency distributions of the other crosses, W202 x D10-1b, W420 x D10-1b, B6693 x Pg-1b, W420 x B6693 and W407 x D10-1b are presented in Tables 16-20. The crosses of W202 x D10-1b, W420 x D10-1b, B6693 x Pg-1b have a pattern of segregation very similar to that of W420 x Pg-1b for SS and DI (Tables 16-18). Population means (Figs. 12-14) for these three crosses also followed a pattern similar to that of W420 x PG-1b for each of the three characters. The small variations which occurred in these generation mean configurations were usually due to the behavior of the backcrosses. The graphical relationship of the parents, F_1, and F_2 usually was close to a straight line, and generally suggested that inheritance was mostly additive. Most deviations from mid-parent values of the F_1 and backcrosses were non-significant (Tables 27-29).

In W420 x B6693 and W407 x D10-1b, which are the resistant x resistant and susceptable x susceptable crosses, respectively, the progeny generations were all skewed toward and strongly overlapping with the parents. Graphed generation means (Fig. 12) generally gave flat configurations and variances were lower (Table 30) for DI and SS, indicating small differences between parents and little segregation in the F_2 and backcrosses. Deviations from mid-parent values (Tables 27-29), for SS and DI were all non-significant for these crosses.

Table 16. Frequency distribution (percentage) for neck-rot disease index, and soluble solids content in a cross between W202 (P_1) x D10-1b (P_2).

	Neck-rot disease index				
	0	1	2	3	4
P_1	42.2	35.9	12.5	7.8	1.5
P_2			14.3	31.7	53.9
F_1		5.7	9.6	40.4	44.2
BC_1	8.4	10.1	28.8	30.5	22.0
BC_2			3.4	17.2	79.3
F_2	7.3	11.5	14.7	27.4	38.9

	Soluble solids (%)					
	6	7	8	9	10	11
P_1		3.1	1.5	28.1	64.0	3.1
P_2	22.2	46.0	26.9	4.7		
F_1	1.7	5.7	25.0	44.2	38.5	3.8
BC_1	1.6	3.4	20.3	37.3	33.9	3.4
BC_2	48.2	31.0	20.6			
F_2	1.0	5.2	15.7	35.7	29.6	9.5

Table 17. Frequency distribution (percentage) for neck-rot disease index and soluble solids content in a cross between W420 (P_1) x D10-1b (P_2).

	Neck-rot disease index				
	0	1	2	3	4
P_1	35.9	34.3	21.8	7.8	
P_2	1.5	4.6	9.4	37.5	46.8
F_1	8.3	16.6	33.3	25.0	16.6
BC_1	14.0	23.4	20.3	26.5	15.6
BC_2	12.7	25.4	29.1	16.3	16.3
F_2	16.8	17.9	20.0	32.6	14.7

	Soluble solids (%)								
	6	7	8	9	10	11	12	13	14
P_1					7.8	25.0	50.0	15.6	1.5
P_2	3.1	15.6	28.1	31.2	12.5	3.1	4.6	1.5	
F_1				16.6	41.6	41.6			
BC_1			1.5	17.2	18.7	34.3	26.5	1.5	
BC_2		5.4	5.4	20.0	40.0	16.3	12.7		
F_2		4.2	2.1	17.9	34.7	24.2	16.8		

Table 18. Frequency distribution (percentage) for neck-rot disease index and soluble solids content in a cross between B6693 (P_1) x Pg-1b (P_2).

	Neck-rot disease index				
	0	1	2	3	4
P_1	26.9	30.1	38.1	4.6	
P_2	1.5	3.1	21.8	29.6	43.7
F_1		36.0	60.0	4.0	
BC_1	9.4	29.6	45.3	10.9	4.6
BC_2	4.6	15.6	29.6	42.2	7.8
F_2	4.3	17.2	29.3	33.6	15.5

	Soluble solids (%)						
	6	7	8	9	10	11	12
P_1		1.5	7.9	15.8	47.6	26.9	
P_2	29.6	31.5	39.0				
F_1	8.0	8.0	28.0	32.0	20.0	4.0	
BC_1		1.5	10.9	26.5	40.6	17.2	3.1
BC_2	7.8	18.7	29.6	37.5	6.2		
F_2		11.2	23.2	33.6	21.5	9.4	0.8

Table 19. Frequency distribution (percentage) for neck-rot disease index, pyruvic acid and soluble solids content in a cross between W420 (P_1) x B6693 (P_2).

	Neck-rot disease index				
	0	1	2	3	4
P_1	28.3	53.3	10.0	3.3	5.0
P_2	10.8	8.7	41.3	28.2	10.8
F_1	38.7	37.1	14.5	4.8	
BC_1	44.4	47.6	7.9		
BC_2	29.0	38.7	22.6	9.6	
F_2	42.9	32.7	21.5	1.8	0.9

	Pyruvic acid (µ moles/g)					
	6	8	10	12	14	16
P_1			15.0	28.3	35.0	21.6
P_2		2.1	91.3	6.5		
F_1			22.5	53.2	22.5	1.6
BC_1			17.4	31.7	39.6	11.1
BC_2		8.0	48.3	37.0	6.4	
F_2		2.8	45.8	33.6	15.8	1.8

	Soluble solids (%)						
	6	7	8	9	10	11	12
P_1		8.3	25.0	43.3	21.6	1.6	
P_2		4.3	17.4	41.3	32.6	4.3	
F_1			3.2	19.4	62.9	14.5	
BC_1				17.4	60.3	22.2	
BC_2			8.1	32.2	38.7	19.3	1.6
F_2		0.9	7.4	21.4	57.0	13.1	

Table 20. Frequency distribution (percentage) for neck-rot disease index and soluble solids content in a cross between W407 (P_1) x D10-1b (P_2).

	Neck-rot disease index				
	0	1	2	3	4
P_1			10.0	23.3	66.6
P_2			12.2	34.6	53.0
F_1			17.9	38.4	43.5
BC_1		1.7	13.5	45.7	38.9
BC_2			3.8	23.0	73.0
F_2		1.0	13.6	37.8	47.3

	Soluble solids (%)				
	6	7	8	9	10
P_1	6.6	20.0	38.3	21.6	13.3
P_2	20.0	30.6	34.6	14.3	
F_1	2.5	33.3	41.0	17.9	5.1
BC_1	1.7	20.3	44.0	27.1	6.7
BC_2	7.6	42.3	26.9	23.0	
F_2	6.3	21.0	33.6	31.6	7.3

Estimates of gene effects

Estimates of mean, dominance and additive gene effects and tests of goodness of fit of the three parameter model were done for three traits (Tables 22-24).

The estimates of gene effects for DI are presented in Table 22. The small and non-significant Chi-square values due to deviations from the model for DI in all of the crosses reveal that the additive-dominance model adequately describes these data and provides no evidence for the presence of epistatic effects. The estimates of additive effects (a) were significant in all of the resistant x susceptible crosses, and were always greater in these crosses than the estimates of dominance effects (d) which were not significant in any cross. Estimates of additive effects in the resistant x susceptible crosses were fairly large relative to the mean effects, suggesting that genes with additive effects for DI were highly associated, most increasing alleles being in the susceptible parents and decreasing alleles in the resistant parents. This was especially true in the cross W420 x Pg-1b.

Neither additive or dominance effects were significant in the resistant x resistant cross (W420 x B6693) and the susceptible x susceptible cross (W407 x D10-1b). This supports the earlier indications from the graphed generation

means (Fig. 12) and the relatively small variances (Table 30) that there was little segregation for DI in these crosses.

The Chi-square value resulting from deviations from the three parameter model for PA was highly significant in the cross W420 x Pg-1b (Table 23) indicating that the additive-dominance model does not adequately describe these data. The values of six parameters were calculated; and tests of significance for each parameter indicated a significant ad (additive x dominance) and dd (dominance x dominance) component in this cross. This deviation from additivity was due to the high PA level of the BC_1 generation in this cross (Fig. 14). This was also reflected in the significant deviation of the BC_1 generation from its mid-parent value (Table 28). The variation for PA in the cross W420 x B6693, in contrast, was adequately described by the additive-dominance model; and the dominance effect was not significant while the additive effect was significant at the 5% level.

The estimates of gene effects for SS are presented in Table 24. The Chi-square tests for deviations from the three parameter model were non-siginificant for all crosses except W202 x D10-1b. The deviations from additivity for SS in this cross are due to the low SS level in the BC_2 generation. This is illustrated graphically in Figure 13 and as well as in Table 29 by the significant deviation of

the BC_2 from its mid-parent value. Hayman (1958) showed that the best approximations of additive and dominance effects are provided by the estimates from the three parameter model even when a significant Chi-square for deviations from the model is obtained. In each of the four crosses where the parents differed significantly in SS content (W420 X Pg-1b, W202 X D10-1b, W420 X D10-1b and B6693 X Pg-1b) the three parameter model estimates of additive gene effects were significant and larger than the dominance effects which were in no case significant. In contrast to the estimates for DI, the additive effects for SS in all crosses were relatively small compared to mean effects, indicating that increasing and decreasing alleles for SS are not highly associated in these parents; that is, some increasing alleles may be present in the low SS parents.

The estimates of gene effects for SS in the cross W420 x B6693 (Table 24) are the only instance in these data where the dominance effect was highly significant while the additive effect was not significantly different than zero. This heterotic response is represented graphically in Figure 13 and is also reflected by the significant deviation of the F_1 from the mid-parent (Table 29).

Table 21. Means of the parents and derived generations of neck-rot disease index, pyruvic acid, and soluble solids content of six onion crosses.

Crosses	Populations					
P_1 x P_2	P_1	P_2	F_1	BC_1	BC_2	F_2
			Disease Index			
W420 x Pg-1b	0.47	3.44	2.76	1.03	2.54	2.18
W202 x D10-1b	0.73	3.25	3.11	2.31	3.64	2.70
W420 x D10-1b	0.84	3.10	2.08	1.88	1.85	1.95
B6693x Pg-1b	1.10	3.04	1.52	1.61	2.18	2.33
W420 x B6693	0.83	2.05	0.89	0.45	0.98	0.70
W407 x D10-1b	3.46	3.39	3.18	3.17	3.62	3.27
			Pyruvic acid (u moles/g)			
W420 x Pg-1b	13.2	8.68	10.91	14.08	9.52	11.44
W420 x B6693	14.2	10.88	13.02	13.75	11.76	12.16
			Soluble Solids (%)			
W420 x Pg-1b	11.78	7.25	10.11	11.95	8.60	9.49
W202 x D10-1b	10.08	7.46	9.38	9.47	7.06	9.65
W420 x D10-1b	12.13	9.09	10.57	11.10	10.33	10.67
B6693x Pg-1b	10.27	7.46	8.95	9.99	8.55	9.34
W420 x B6693	9.32	9.50	10.30	10.43	10.19	10.10
W407 x D10-1b	8.56	7.79	8.26	8.52	8.06	8.47

Table 22. Estimates of genes effects for neck-rot disease index from generations means of six onion crosses, using a three parameter model.

Crosses	Genes effects[z]			
	m	a	d	X^2
W420 x Pg-1b	2.1**	-1.5**	0.5	3.41 NS
W202 x D10-1b	2.7**	-1.3*	1.1	2.2 NS
W420 x D10-1b	3.4**	-1.0*	0.1	0.27 NS
B6693x Pg-1b	1.5**	0.9*	-0.6	1.47 NS
W420 x B6693	0.9*	-0.2	-0.8	2.21 NS
W407 x D10-1b	3.3**	-0.1	0.2	0.02 NS

[z] Gene effect: m = mean, a = additive, d = dominace, X^2 = chi-square.

* Significant at 5 % probability level.
** Significant at 1 % probability level.
NS Non-significant.

Table 23. Estimates of genes effects for pyruvic acid content from generations means of two onion crosses, using three and six parameter model.

Crosses	Genes effects[z]					
	Three parameter model					
	m	a	d	X^2		
W420 x Pg-1b	9.2**	2.7**	0.2	29.9 **		
W420 x B6693	11.8**	1.7*	0.5	3.16 NS		
	Six parameter model					
	m	a	d	aa	ad	dd
W420xPg-1b	9.6**	2.3**	6.2*	1.4	4.6**	-4.9*

[z] Gene effect: m = mean, a = additive, d = dominace, X^2 = chi-square, aa = additive x additive, ad = additive x dominance, dd = dominace x dominace.

* Significant at 5 % probability level.
** Significant at 1 % probability level.
NS Non-significant.

Table 24. Estimates of genes effects for soluble solids content from generations means of six onion crosses, using three and six parameter model.

Crosses	Genes effects[z]			
	Three parameter model			
	m	a	d	X^2
W420 x Pg-1b	9.9**	2.4**	0.7	3.30 NS
W202 x D10-1b	8.7**	1.5**	0.3	7.80 *
W420 x D10-1b	10.6**	1.6*	-0.1	0.30 NS
B6693x Pg-1b	9.1**	1.5**	0.3	1.95 NS
W420 x B6693	10.0**	0.5	4.4**	2.50 NS
W407 x D10-1b	12.7**	1.1	0.1	0.30 NS

	Six parameter model					
	m	a	d	aa	ad	dd
W202xD10-1b	14.3**	1.3**	-13.6**	-5.5**	2.2**	8.8**

[z] Gene effect: m = mean, a = additive, d = dominace, X^2 = chi-square, aa = additive x additive, ad = additive x dominance, dd = dominace x dominance.

* Significant at 5 % probability level.
** Significant at 1 % probability level.
NS Non-significant.

Heritability

Estimates of broad sense heritability ranged from 15% to 63% for DI, 48% to 53% for PA, and 8% to 56% for SS (Table 25). The heritability values obtained from the individual crosses were related to the degree of differences in the traits between parents. Higher values of heritability were obtained in the crosses which had large parental difference in SS and DI. The broad-sense heritability of DI and SS were very low in the cross W407 x D10-1b. Selection for the three traits should be relatively more effective in crosses having large parental difference than where parental difference are small.

Correlations among traits

Phenotypic and environmental correlations among DI, PA and SS were estimated using parental, F_1 and F_2 data from the cross W420 x Pg-1b (Table 26). The correlation between PA and SS was moderately positive ($r = 0.49$) and highly significant. This is similar to the estimate obtained in the diallel experiment and again reflects an association between increasing pungency and increasing soluble solids concentration. The correlation coefficients estimated between SS and DI and between PA and DI were both small and negative and not significantly different than zero. Although the negative values of these statistics may support

the significant negative correlations estimated for these traits in the diallel experiment, the associations appear to be weaker in this material. This may reflect genetic recombination in the segregating F_2 population.

The significant environmental correlation between PA and DI suggests that PA and DI were, to a degree, similarly affected by environmental fluctuations within the experiment.

Table 25. Broad-sense heritability estimates for neck-rot disease index, pyruvic acid, and soluble solids content of six onion crosses.

Crosses	Broad-sense heritability (%)		
	Disease index	Soluble solids	pyruvic acid
W420 x Pg-1b	63	56	53
W202 x D10-1b	54	49	--
W420 x D10-1b	42	41	--
B6693x Pg-1b	56	34	--
W420 x B6693	62	13	48
W407 x D10-1b	15	8	--

Table 26. The phenotypic (r_p) and environmental (r_e) correlations among onion neck-rot disease index, pungency (pyruvic acid), and soluble solids content estimated from parents, F_1, and F_2 data in the cross W420 x Pg-1b.

		Traits	
traits	Statistic	Soluble Solids	Pungency
Pungency	r_p	0.49**	----
	r_e	0.06	----
Neck-rot disease index	r_p	-0.12	-0.17
	r_e	-0.09	-0.16*

* Significant at 5 % probability level.
** Significant at 1 % probability level.

Table 27. Deviation in mean neck-rot disease index of the F_1 generation and backcrosses from their mid-parent values.

Crosses	Deviation in disease index		
	F_1 - MP	$BC_1-(F_1+P_1)/2$	$BC_2-(F_1+P_2)/2$
W420 x Pg-1b	0.81 NS	-0.58 NS	-0.56 NS
W202 x D10-1b	1.12 *	0.39 NS	0.46 NS
W420 x D10-1b	0.11 NS	-0.42 NS	-0.74 NS
B6693x Pg-1b	-0.55 NS	0.30 NS	-0.10 NS
W420 x B6693	-0.55 NS	-0.41 NS	-0.49 NS
W407 x D10-1b	-0.24 NS	-0.15 NS	-0.34 NS

* Significant at 5% probability.
** Significant at 1% probability.
NS Non-significant.

Table 28. Deviation in mean pyruvic acid content of the F_1 generation and backcrosses from their mid-parent values.

Crosses	Deviation in μ moles/g		
	F_1 - MP	$BC_1-(F_1+P_1)/2$	$BC_2-(F_1+P_2)/2$
W420 x Pg-1b	-0.04 NS	2.03 **	-0.28 NS
W420 x B6693	0.48 NS	0.14 NS	-0.19 NS

* Significant at 5% probability.
** Significant at 1% probability.
Non-significant.

Table 29. Deviation in soluble solids content of F_1 generation and backcrosses from their mid-parent value of six onion crosses.

Crosses	Deviation in percent soluble solids		
	F_1 - MP	$BC_1-(F_1+P_1)/2$	$BC_2-(F_1+P_2)/2$
W420 x Pg-1b	0.60 NS	1.01 *	-0.08 NS
W202 x D10-1b	0.61 NS	-0.26 NS	-1.36 **
W420 x D10-1b	-0.04 NS	-0.22 NS	0.50 NS
B6693x Pg-1b	0.09 NS	0.38 NS	0.35 NS
W420 x B6693	0.89 *	0.62 NS	0.29 NS
W407 x D10-1b	0.09 NS	0.11 NS	0.04 NS

* Significant at 5% probability.
** Significant at 1% probability.
NS Non-significant.

Table 30. Variances of the parents and derived generations of onion neck-rot disease index, pyruvic acid, and soluble solids content of six onion crosses.

Crosses	Populations					
P_1 x P_2	P_1	P_2	F_1	BC_1	BC_2	F_2
		Disease Index Variance				
W420 x Pg-1b	0.38	0.51	1.44	1.11	1.32	1.78
W202 x D.10-1b	0.90	0.66	0.75	1.40	0.32	1.68
W420 x D.10-1b	0.73	0.85	1.63	1.77	1.72	1.75
B6693x Pg-1b	0.80	1.00	0.42	0.90	0.98	1.58
W420 x B6693	0.92	1.27	1.11	0.27	0.81	0.67
W407 x D.10-1b	0.47	0.48	0.53	0.53	0.40	0.58
		Pyruvic acid Variance				
W420 x Pg-1b	2.42	1.18	1.56	2.20	2.25	3.53
W420 x B6693	3.76	0.43	1.47	2.90	1.93	2.58
		Soluble solids Variance				
W420 x Pg-1b	0.66	0.44	0.74	0.51	1.25	1.35
W202 x D.10-1b	0.44	0.59	1.08	0.81	0.45	1.28
W420 x D.10-1b	0.68	1.88	0.52	1.17	1.46	1.47
B6693x Pg-1b	0.80	0.59	1.27	1.03	1.13	1.28
W420 x B6693	0.86	0.91	0.40	0.34	0.76	0.60
W407 x D.10-1b	1.17	0.89	0.69	0.78	0.63	0.98

V. GENERAL DISCUSSION

Resistance to neck-rot, pungency, and dry matter content are important characters of onion. Botrytis neck-rot causes large losses in stored onions worldwide, especially in non-controlled storage conditions and during export shipments. Depending on the intended use of onions, either pungent or mild onions may be desired. There has been considerable effort by onion breeders to increase the dry matter content in new cultivars for dehydration and also to develop sweet and mild onions for fresh raw uses. It would be desirable to combine each of these traits with improved resistance to neck-rot.

Significant heritable differences in neck-rot resistance, pungency and soluble solids content were observed among the inbred lines, F_1 hybrids and segregating generations in the present study (Tables 9-11 and Table 21). This is in agreement with the observations of Munn (1945), Groenendijk and Pietiet (1962) and Miyaura et al (1985) that variation for these traits is genotype dependent.

Pal and Singh (1987) reported that additive gene effects were most important in the inheritance of pyruvic acid in onions; and Owen (1961) found that cumulative gene action was most important in the inheritance of soluble solids content of onions. In the present study, the

additive effects of genes were of major importance in the variation among parental lines and their F_1 hybrids for all three traits studied. General combining ability was the most significant factor in determining levels of neck-rot resistance, pungency and soluble solids of F_1 hybrids in the diallel cross (Table 13). Additive gene effects were highly significant in determining levels of these characters in F_1 generations derived from the six crosses of onions (Tables 18-20). The segregation patterns (Figs. 9-11) and the graphical representations of the generation means (Figs. 12-14) also generally indicated additivity in these crosses.

Specific combining ability was also significant for the traits studied, although apparently of lesser importance than general combining ability (Table 13). However, the pattern of heterosis for increased neck-rot resistance and lower pungency observed in the diallel hybrids compared to their parents is a significant and potentially useful departure from additivity in these data (Tables 6 and 7). This heterotic pattern was not observed for soluble solids content (Table 8); and the high GCA/SCA mean squares ratio for soluble solids content also reflected a lack of dominance or heterosis for this trait (Table 13).

Broad-sense heritability estimates for SS ranged from 8% in a cross between parents having 7.8% and 8.6% SS to 56% in a cross between parents having 7.2% and 11.8% SS (Table 25). Warid (1952) reported a heritability estimate of 71%

for soluble solids in a cross between parents having 6% and 16% SS. This association between genetic difference between the parents and the magnitude of broad-sense heritability was also observed for neck-rot resistance where estimates ranged from 15% in a cross between susceptible parents to 63% in the cross between the most resistant and the most susceptible parents (Tables 21 and 25). Broad-sense heritability estimates of 48% and 53% were determined for PA in two crosses in which the parents differed in PA by about the same amount in each case (Tables 21 and 25).

Earlier investigators have reported that pungent cultivars were more resistant to neck-rot disease (Owen, 1950), that pungency and soluble solids were positively correlated (Schwimmer and Guadagni, 1962) and that mild flavor, poor keeping quality and low dry matter were associated (Foskett, 1950). These correlations are of critical importance to plant breeders attempting to develop varieties with various combinations of these traits.

Existence of these correlations was confirmed in the present study. From the diallel data, significant correlations of 0.57 for SS with PA, -0.63 of SS with DI and -0.35 of PA with DI were estimated (Table 14).

Although significant, breeders may be encouraged in that these correlations are only moderate in strength; and the negative correlation between PA and DI was the smallest of the three. Several of the diallel hybrids exhibited

combinations of traits that were in opposition to the direction of this correlation. Hybrids B6693 x M8155, B6693 x P6502 and P6502 x W420 all had notably low DI and PA values (Table 12). The least pungent hybrid in the diallel (M8155 x P6502) was not among the most susceptible to neck-rot, but rather had an intermediate DI value. Parent M8155 exhibited a particularly favorable combination of GCA for low pungency and neck-rot resistance (Tables 9 and 10).

The correlations of PA with DI and SS with DI determined from the F_2 generation of the cross W420 x Pg-1b were small, negative and not significantly greater than zero (Table 26). This is a weaker association of these traits than was observed in the diallel inbred parents and their F_1 hybrids. These differences may be due to genetic recombination in the F_2 population. This suggests that selection for low DI and low PA or low DI and low SS in appropriately structured segregating populations could be effective.

The correlations estimated from both the diallel data and the F_2 data between PA and SS were positive, moderate and significant (0.57 and 0.49, respectively). Because the compounds responsible for onion pungency also contribute to total dissolved solids, at least part of this positive correlation is due to the partial identity of the two traits. In the breeding of onion varieties for dehydration where both high soluble solids and high flavoring strength

are desired, selections based on soluble solids (a relatively rapid determination) can also be expected to increase pungency (a more expensive determination).

Breeding methods

The onion breeder desiring to improve populations derived from the genetic material used in this study should employ selection procedures that most effectively use additive genetic variance. In addition, the small and non-significant correlation between pungency and DI observed in the segregating F_2 population in this study indicates that it may be most effective to select for low pungency and neck-rot resistance after genetic recombination. Both mass selection and recurrent selection procedures would allow opportunity for recombination and make use of additive genetic variance.

The pattern of heterosis for low neck-rot disease index and low pyruvic acid content observed in the diallel cross hybrids suggests that the development of hybrid varieties may be an effective way to exploit non-additive genetic variance displayed in this study.

VI. SUMMARY and CONCLUSIONS

A. Results of the diallel analysis indicated that:

1. Negative heterosis for DI suggested that F_1 hybrids exhibited more resistance to neck-rot than their parents.
2. F_1s were significantly less pungent than their parental mean when high pungency inbreds were used as either parent.
3. Non-significant and very small levels of heterosis suggested that primarily additive genes controlled SS. When high SS parents were used, F_1 progeny means were significantly below the mean of the common parent.
4. General combining ability values for DI, SS, and PA were highly significant and much higher than values for specific combining ability, suggesting that additive genetic variance was more important than non-additive genetic variance, especially for SS.

B. Analysis of segregating generations indicated that:

1. DI, SS, and PA were each inherited in a quantitative manner.
2. F_1 and F_2 frequency distributions for W420 x Pg-1b indicated slight dominance of neck-rot susceptibility, highly additive inheritance of SS and a small degree of negative heterosis for PA, possibly associated with F_1

hybrid vigor.

3. With minor exceptions, the relationships of generation means supported additive inheritance of DI, SS, and PA.
4. Generation Means Analyses indicated that additive inheritance was most important for DI, SS, and PA, but significant epistasis was involved in PA, and to a minor extent in SS. Relative large additive effects relative to mean effects suggested that additive genes for DI were highly associated, but this relationship was not indicated for SS and PA.
5. Broad sense heritability estimates for soluble solids ranged from 15% to 63% for neck-rot disease index, 48% to 53% for pyruvic acid, and 8% to 56% for soluble solids.

C. Analyses of both the diallel cross and segregating generations generally indicated a strong positive association between PA and SS, a small negative relationship between PA and DI, and a moderate negative association between DI and SS. A significant environmental correlation between PA and DI suggested that PA and DI were, to a degree, similarly affected by environmental fluctuations.

D. Selection for high pungency in onions can be easily and cheaply done by testing for SS by means of refractive index.

E. Small and non-significant correlation between PA and DI

in the segregating generations suggest that there is a possibility for development of low pungency onions with less neck-rot susceptibility.

F. Predominate additive inheritance of DI, SS, and PA indicate that mass and recurrent selection procedures should be effective. Recombinations of additive genes can be expected from crossing superior lines and selection in later generations.

G. The limited heterosis observed for low neck-rot disease index and low pungency in the diallel cross may be utilized in some specific F_1 hybrid combination.

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