GENETIC EVALUATION OF FIVE GUAVA CLONES BY DIALLEL ANALYSIS

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LIST OF ABBREVIATIONS

HKP = 'Hong Kong Pink'

'Allahabad' = 'Allahabad Safeda'

KHK = 'Ka Hua Kula'

R x S = 'Ruby x Supreme'

CV = Coefficient of Variation

SCA = Specific Combining Ability

GCA = General Combining Ability

Locat = Location

Enz = Enzyme

Diam = Diameter

TSS = Total Soluble Solids

L* = Lightness

CHAPTER 1
INTRODUCTION

History and Botany

The tropical guava is a small to medium sized tree in the Myrtaceae plant family. *Psidium guajava L.* is the most important member of the genus, although many of the other species bear edible fruits (Ruehle,1948; MacCaughey, 1917). All are neotropical in origin. The guava exhibits great variability in fruit characters. This prompted early taxonomists to distinguish several species based on fruit shape. In fact, the diversity of types all belongs to the same species (Wilson, 1980). This diversity has resulted in a plethora of opinions about the characteristics of a good guava. The early and widespread dissemination of this fruit by Spanish and Portuguese explorers added to the confusion by exposing a great number of cultures to the guava. Distinct types became highly esteemed in different regions of the tropical world. This is likely attributable to the phenomenon of genetic drift due to limited seed or clone introductions.

The greatest diversity of fruit types exists in the new world tropics, and consequently numerous culinary uses have arisen (Ruehle,1948). In contrast, India and southeast Asia have a much narrower genetic base. Particular types such as 'Allahabad Safeda' in India and crisp green varieties in Asia dominate the market. The majority are consumed as fresh fruit.

Hawaii also has a limited guava gene pool. The early introductions were soft, pink types best for processing. As a result, the local people developed a taste for guava preserves and drinks. The acid, seedy qualities of the majority of introduced types were not conducive to fresh consumption. Later introductions of selected varieties from Florida and elsewhere improved the genetic base of guava in Hawaii (Nakasone et al., 1967). Local selections, for puree production, such as 'Beaumont,' as well as thick-fleshed introductions, provided impetus for growers to plant guavas more extensively. Collection of fruit from wild trees had resulted in inconsistent puree quality, a problem which was later alleviated by planting improved cultivars (Shigeura, 1983).

Hawaii

Since the early 1970's, commercial acreage of guavas has expanded to include about 1100 acres at present (Statistics of Hawaiian Agr, 1991). Producing areas exist around the state, but the majority of the acreage is on Kauai and near Hilo. 'Beaumont' is still the most common variety, although higher quality selections are gaining favor. Production exceeds 7000 tons, nearly all for processing into nectars and jellies. Puree recovery plants operate year round due to orchard practices of cycling fruit production (Bittenbender, 1991; Shiguera 1983). Efforts to market guava drinks on the mainland have been slow, but local consumption has increased over the years. However, larger markets will be required to support

currently expanding production. Producers on Kauai frequently have surplus puree due to oversupply in local markets (J. Gushiken, personal communication). The mainland, Canada, Japan and Mexico are viable markets with large consumer demand for juice products. Success of the Hawaiian industry may rely on the exploitation of these markets. Diversification of guava products can also bolster the guava industry. Guava paste, candy, canned shells, syrup and other confectionary items could become just as common on the mainland as other popular fruit products. In order to create such a scenario, the growers must be able to maintain consistent levels of quality and productivity. Producing cultivars which meet the demands of the growers, processors and consumers requires a well organized fruit breeding program.

Guava Improvement

In the case of the guava, numerous goals for breeding have been recognized in Hawaii. Input from growers, consumers and scientists influences the priority given to specific areas of research (Bittenbender, 1991; Nakasone, 1976). Improving fruit quality is the motivation behind the various breeding strategies. All other characteristics under selection ultimately must be linked to good fruit quality. In Hawaii the most important of these are considered to be resistance to pests and pathogens, fruit size, sugar and acid content, seediness, color, productivity, tree habit and fruit handling characteristics.

Disease Resistance

Resistance to pests and pathogens is a major concern in Hawaii, due to the benign climate and diversity of introduced diseases and insects. Fungal and bacterial rots affect guava fruit in wet regions of the state. Because most production occurs in such areas, rot is a serious problem with varieties such as 'Beaumont'. The fungal pathogen, *Mucor hiemalis*, causitive agent of *Mucor* rot, is the most important problem reported to date (Kunimoto et al, 1977). It is often related to insect damage such as the oviposition sites from various fruit flies which infest guava (Ito et al, 1976). Any wound site on the fruit permits the fungal spores to invade. Resistance to this pathogen has been observed in some cultivars of guava. The resistance was highest in sweet, dessert types (Ito et al, 1976). Cell wall strength and levels of volatile compounds in the pericarp may both deter infection. Genetic factors controlling these traits as well as wound response most likely play an important role. The operation of numerous genes in providing quantitative resistance to disease attests to the importance of initiating a recurrent breeding program.

Currently, several dessert varieties, such as 'Allahabad Safeda' and 'Ruby x Supreme,' (R x S) have proven to be resistant to the *Mucor* fungus (Ito et al., 1976). These were selected as two of the parents for the current diallel experiment. 'Hong Kong Pink' (HKP) was selected as the third dessert-type parent due to its thick flesh and

small seed cavity. The other three parents, 157, 180, and 'Ka Hua Kula' (KHK) are acid, processing selections, susceptible to mucor and various other softrots. Although the only serious disease to date is *Mucor* rot, the possibility of serious crop losses from other pathogens in the future is always a threat. Developing resistance to a wide array of bacterial and fungal diseases should be a priority at the present time, not after the fact.

No serious viral diseases of guava have been detected in Hawaii but the presence of a mycoplasm is suspected to reduce the vigor of some trees (W. Borth, personal communication). Genetic resistance to such organisms is virtually unknown but as research continues, molecular genetic techniques may change this situation. Naturally occurring resistance may yet be identified. Screening a wide assortment of germplasm will be necessary and essential to increase the success of the breeding program.

Insect Resistance

Insect pests are a serious problem in guava production. Because the fruit is processed whole, external damage is more significant than in fruits with disposable exocarps. Red-banded thrips (*Selenothrips rubrocinctus*), mites, aphids, scale and mealybugs all damage the fruit exterior, while Chinese Rose beetles (*Adoretus sinicus*) attack the young foliage (Shigeura et al., 1983). In order to avoid extensive use of pesticides, the selection of resistant varieties is important. Resistance may be associated with

cutinous layers, volatile compounds, and toxic alkaloids on the fruit and leaf surfaces (Ahmed et al., 1983). Varieties with glaucous fruit exocarps seem to exhibit more resistance to mites and thrips than varieties with thin cutinous layers. More evaluation of varieties for insect resistance needs to be undertaken. The infestation of guava fruit by several types of fruit flies demands such an effort.

Asian and Mediterranean fruit flies are a widespread threat to guavas in Hawaii (Shigeura et al.,1983). The deposition of eggs and subsequent larval development often ruins the fruit. The oviposition sites also provide a favorable location for infection by fungal or bacterial pathogens. The high susceptibility of guavas to these flies has restricted the production of fruit for fresh consumption in Hawaii. At present, no varieties exhibit resistance to fruit flies. In fact, the varieties with the thickest, toughest exocarps seem to be the most susceptible (R.A. Hamilton, personal communication). A practical approach may be to search for varieties with high levels of volatile compounds in the skin which may deter the flies. Quality decline is obviously severe under conditions of heavy fruit fly infestation. Developing resistance to flies and all of the other arthropod pests is crucial to maintain the highest possible fruit quality.

Flavor Constituents

Improving organoleptic characters is another step in the process of developing high quality guavas. The levels of flavonoids and other organic compounds which create the unique aroma and flavor of the guava are highly variable. Wilson lists 46 volatile flavor components isolated from guava (1980). He concludes that cinnamyl acetate has the strongest influence on guava aroma. Soluble solids, citric and ascorbic acids, and moisture content also fluctuate to a great degree. Constituents of flavor and aroma are not easy to evaluate genetically as they vary not only due to genotypic interactions but also in response to the environment. However, sugar and acid levels are of primary interest to growers. The measurement of these characters and evaluation of parental influence on their levels in hybrid progeny is one of the major goals of the current experiment.

Color

In addition to flavor, color and texture are important characters which vary a great deal. Guavas exhibit a range of colors, including: white, salmon, yellow, pink, red and even dull orange. In Hawaii, pink to red is the desired range, especially for processing (Hamilton et al., 1954). Other countries are less finicky, but manipulation of color producing genes would increase the variety for the consumer. After evaluating 500 F1 hybrids between red and

white guavas, Subramanyam and Iyer (1992) concluded that color is a monogenic trait and red is dominant to white. However, the level of the red pigment, lycopene, fluctuates in response to the environment. Therefore, evaluating genotype by environment interactions will be necessary to identify individual varieties with consistently high pigment levels. Measuring pulp color with a colorimeter quantifies the various light spectrum components, producing data for statistical analysis.

Texture

Texture and consistency can be measured based on parameters such as water content, pectin content or stone cell content. However, much easier evaluations by visual or physical means were deemed sufficient for the current experiment. These characters affect the post harvest physiology, and consumer perception of quality for fresh fruit. Resistance to bruising and shelf life are linked to fruit texture. Thick fleshed, firm fruits have a longer shelf life than thin, soft or watery fruits. Watersoaking and blossom end rot often relate to calcium assimilation in the cell walls. Resistance to cell wall decay and fruit firmness are characteristics which need to be evaluated in the breeding program.

Size and Seediness

Two other factors which relate to fruit quality are size and seed content. Size can be measured in several ways. The diameter of the fruit and the diameter of the seed cavity are useful values. A small seed cavity in relation to the fruit diameter corresponds to fewer seeds. Thick mesocarp and small seed cavities are very desirable qualities for all guavas. Less of the fruit is wasted in processing. Consumers also prefer fewer seeds in guavas for fresh consumption. Large fruits are also desirable for the fresh market, although size is less significant to processors. Size does not determine fruit weight. Large fruit may be puffy, and have thin mesocarps. The weight depends on density of the flesh. The mesocarp is more dense than the seed cavity. Therefore, thick fleshed varities with fewer seeds are usually heavy in relation to size. Moisture content ultimately determines weight.

Yield

This character varies a great deal among guavas. An important goal of the breeding program is to develop high yielding varieties with good fruit qualities. A perfect fruit is worthless to the grower if the tree only produces ten fruits each year. This is actually a

common shortcoming of desirable selections as well as polyploid, seedless guavas (Wilson, 1980). Varieties such as 'Beaumont' have displayed excellent yields under Hawaiian conditions (Nakasone et al., 1976). The genetic components of yield can be determined in a breeding program. This information can be utilized to transfer genes which contribute to high yield into varieties with good fruit quality (Subramanyan and Iyer,1992). Yield trials must be established under normal orchard practices. Screening numerous varieties, and hybrid selections under local conditions is a crucial step in the breeding program.

Past Breeding Achievements

Seedling Selection

Guava breeding efforts in the past have relied heavily on seedling selection. Numerous cultivars with good quality fruit have been selected from both open pollinated and hybrid progenies. A hybrid breeding program was initiated in Florida by Ruehle during the 1940's. His efforts produced some high quality cultivars like 'Ruby Supreme,' 'Red Indian,' 'Pink Acid,' 6362 and 6363 (Ruehle,1948). The selection program focused on fruit quality, not on genetic characterization of various traits. The same is true of most cultivars developed in Hawaii. Dr. J.H. Beaumont, Dr. R.A. Hamilton and Dr. H.Y. Nakasone all evaluated various guava seedlings in Hawaii (Shigeura et al.,1983). Numerous trees with good fruit

quality were named. Dr. Nakasone evaluated over 1200 seedlings of 'Beaumont' and identified several good processing types. Efforts to quantify genetic traits were not attempted, although several desirable characteristics were connected to particular cultivars. Resistance to red-banded thrips and *Mucor* rot are examples. Lack of inbred clones was one of the limiting factors which still exists. However, from the standpoint of fruit quality, the past research was quite successful in developing good varieties. 'Beaumont', KHK and 'Waiakea' have been successfully incorporated into Hawaiian guava orchards. These varieties all possess desirable qualities and the experience gained from their performance is valuable input to the current breeding program.

Cytology

Cytogenetic research has been an important component of the various efforts to develop superior guava cultivars. Studies of chromosome behavior have revealed the existence of numerous guava polyploids and provided clues about species relationships in the genus Psidium. Guava is one of the few diploids identified in the genus with 2N = 22. However, variations from this ploidy level have been found. Raman (1971) described chromosome morphologies and behavior in diploid and triploid Indian guava varieties. Triploid types may produce seedless fruit, a desirable character. The authors concluded that both gametic sterility, due to uneven chromosome pairing and genic sterility inhibit seed development. If the nature of

the genetic control over sterility could be elucidated, a wider selection of seedless cultivars could be developed. Artificially induced polyploids can be utilized for the same purpose. The effects of polyploidy in guava, however, may not be as desirable as in other crops. Fruit size often diminishes as does the productivity of the tree (Srivastava, 1977) . Deformed fruit are also very common (Wilson, 1980). If a high quality, well shaped, seedless dessert guava could be developed through polyploid breeding, lower productivity could be offset by higher value per fruit.

Despite limited efforts in cytogenetic research to date, it deserves more attention. Karyotyping and chromosome mapping can provide valuable information about behavior of interesting genes. In addition, chromosome evolution and interspecific variation can be studied. Interspecific hybrids between guava and *Psidium cujavillus* were developed in Hawaii (Hirano and Nakasone, 1969). Some of these expressed characteristics intermediate between the two parents. Interspecific compatibility can be a valuable tool in polyploid breeding. Valuable genetic traits present in other *Psidium* species may be transferable to guava if cross compatibility exists.

CHAPTER 2

MATERIALS AND METHODS

Parent Selection

The evaluation of six guava clones for utility in a breeding program was the intention of this experiment. The selection criteria for the parents included suitability for processing or fresh eating, adaptation to Hawaii, productivity, and disease resistance. No single clone ranked highly in all these categories, but each possessed several superior characteristics. Table 1 lists some important characteristics of the parents. Two of the sweet clones, 'Allahabad' and R x S, exhibited resistance to *Mucor* rot (Ito et al.,1976). In addition R x S and HKP have thick ovary walls and small seed cavities. All are considered dessert types, but 'Allahabad' consistently produces the highest levels of soluble solids.

In contrast the other three parents, KHK, 157 and 180 are processing types with moderate soluble solids levels and high acidity. These clones are susceptible to *Mucor* rot. All 6 clones produce medium to large fruit but productivity varies considerably. KHK is the most productive under Hawaiian conditions (Nakasone et. al., 1976). 'Allahabad' resists both fruit flies and russeting insects better than the other clones (Ito et al., 1976). Breakdown of cell walls and watersoaking have been observed in 157 and 180 in research plantings. Blossom end rot can affect all of the clones, but

TABLE 1. FRUIT QUALITY CHARACTERISTICS OF SIX PARENT CLONES OVER SEVERAL LOCATIONS

Variety	Locat.[a]	Fruit Diam. (cm)	Cavity Diam. (cm)	Fruit Weight (g)	Seeds %	Acid %	Soluble Solids %	Color
097	Waim.[b]	6.97	--	201	--	1.18	8.60	Pink
	Poam.	6.30	3.20	175	2.2	1.49	8.10	Pink
157	Waim.[b]	7.15	--	221	7.4	2.48	10.50	Pink
	Poam.	6.78	4.86	181	2.1	3.40	9.60	Pink
	Wail.[b]	6.57	--	180	7.5	2.50	10.70	Pink
180	Waim.[b]	6.50	--	179	5.5	2.03	10.90	Pink
	Poam.	6.40	4.40	145	2.9	2.33	9.40	Pink
	Wail.[b]	6.16	--	169	6.8	2.30	10.50	Pink
HKP	MaKi.[b]	7.60	4.00	218	1.8	0.20	10.00	Pink
R x S	Poam.	7.28	4.05	220	2.5	0.89	10.00	Pink
Allahabad	Waim.[b]	7.50	5.00	173	3.2	0.60	12.50	White
	Poam.	7.92	5.20	266	1.3	1.05	11.70	White

a - locations: Waim = Waimanalo, Poam = Poamoho, Wail = Wailua, MaKi = Malama Ki

b - data from Nakasone (1967)

'Allahabad' is the least susceptible (H.Y. Nakasone, personal communication).

Breeding Strategy

The traits which characterize the parent clones should be visible to various degrees in their progeny. One way to quantify the genetic control of these traits is to intercross the parents and evaluate their hybrid progeny for the same traits. Progeny performance can provide an indication of the parent's capacity to transmit the traits in question. This step was carried out following parent selection.

Clones of the six parents from Magoon facility were intercrossed to produce all possible F1's, including reciprocals. Seed was collected from mature fruit and seedlings were raised in small plastic containers. Two crosses, HKP x KHK and HKP x 180, failed to produce fruit and were not planted in the field. The other crosses were planted in a six entry diallel at Waimanalo research farm in 1989. This consisted of three replications with four trees per cross in each. The reciprocals were included but not the parents. The soil at the site is a Waialua clay variant of pH 5.8.

After establishing the diallel, some doubt about the identity of the parent clones arose. The labeling of clones at Magoon facility led to confusion. An assortment of different label types as well as inconclusive phenotypic distinctions prompted the initiation of a more accurate identification process. The guava clones at Magoon

and the diallel seedlings at Waimanalo were subjected to systematic isozyme analysis.

Isozyme Electrophoresis

Young leaves from each tree were collected and labeled a day or two prior to the analysis, and stored at 4 C. Potato starch gels (12.5%) were prepared using a histidine citrate (pH 6.5) buffer system (Cardy et al.,1983) consisting of 0.016 M histidine (free base) and 0.002 M citric acid (anhydrous). The gels were wrapped with plastic to prevent dessication and stored at room temperature. Prior to loading samples, the gels were cooled to 4 C.. Leaf samples were homogenized by grinding small discs of tissue along with several drops of an extraction buffer, modified to compensate for very high levels of phenolic compounds in guava (Aradhya, 1992). Extracts were absorbed onto 3 x 10 mm filter paper wicks (Whatman Chroma 3 MM) and inserted into a vertical slit at the cathodic end of the horizontal gel. Anode and cathode were connected to separate trays filled with buffer consisting of 0.065 M histidine and 0.007 M citric acid. The gel was placed with its vertical arms submerged in the buffer, allowing the current to pass from the buffer through the gel. The isozymes were electrophoresed for five to six hours at a constant 15V/cm and 40-50 ma. The gels were removed and sliced horizontally into 1-mm sections. These were histochemically stained for aconitase, aldolase, isocitrate dehydrogenase, leucine aminopeptidase, malate dehydrogenase, phosphoglucoisomerase and

phosphoglucomutase (Arulsekar et al, 1986; Shaw and Prasad, 1970). After an hour of incubation at 37 C, the gels were scored for the various alleles associated with each isozyme. Each individual had a distinct zymotype (isozyme genotype) which could be used to distinguish it from other trees.

Fruit Quality Assessment

Phenotypic evaluation of the fruits included weight, diameter, seed cavity diameter, TSS, % acid, seed weight, and puree color.

Four to eight fruits were collected from each tree, based on availability. The fruits were picked slightly green to avoid unnecessary damage during transport to the lab. Prior to taking measurements the fruit were allowed to ripen in the lab. After ripening the fruit were wiped clean with a towel. Each fruit was weighed on a Mettler 2440 digital scale and the value recorded in grams. Next the fruit were cut in half and the diameter and seed cavity diameters were measured in centimeters. Comments about fruit aroma, insect and disease damage, shape and appearance were recorded as well. Fruits without severe fruit fly infestations were then placed in a Cuisinart food processor and pureed for 30 seconds to one minute. Small samples from the puree were utilized to make chemical measurements.

A small amount of puree, between 1 and 1.8 grams, was diluted with 40 ml of distilled water to facilitate pH measurement. Titration was carried out with a Mettler DL 12 automatic titrator.

The exact weight of puree used was input into the memory along with the titration endpoint of pH 8.1. The machine calculated initial pH and then titrated with 0.1 N sodium hydroxide. After reaching the designated end pH, it calculated % acid in citric acid equivalents, based on the following equation:

$$\% \text{ acidity} = \frac{(\text{ml base})(\text{normality of base})(\text{meq. wt. acid})100}{(\text{g sample})}$$

After the titration, undiluted pH was measured by inserting the electrode directly into the puree.

Soluble solids measurements were taken from undiluted puree using an Atago digital refractometer. Distilled water was used as a zero value prior to each measurement.

Color was evaluated by placing a small amount of puree in a petri dish onto a Hunterlab colorimeter. The values recorded were those from the Hunter L a b scale.

After this final test, the puree was rinsed from the seeds in a collander. The remaining material was washed in a large beaker. After the seeds settled the refuse was poured off and the seeds were blotted dry on a paper towel. The seed weight was recorded in grams and divided by the number of fruits used to obtain an average seed weight. This value was then divided by the average fruit weight to arrive at % seed weight per fruit.

Extra fruits from individual trees were distributed within the lab for input about flavor and aroma from different persons.

Procuring Data

Data collection took place during the spring and fall fruiting seasons of 1992. After the spring harvest, the trees were pruned to induce new growth flushes and flowering in May and June. This led to development of a new crop in late fall 1992 and early winter 1993. In both seasons, fruit were collected and placed in plastic bins for transport to the lab in the morning hours. Notes about tree vigor, productivity, size and pathological problems were made in the field. All fruit evaluation took place in the lab. Data were transferred to computer shortly after the lab evaluations. All empirical values were entered into a Quattro Pro 4.0 spreadsheet to facilitate statistical analyses. Observations about individual tree characteristics were placed in a separate, Excel 3.0 spreadsheet.

Data Analyses

Evaluation of the fruit from the 137 trees provided data sets for eight different traits. The traits were percent total soluble solids, percent acidity, percent seed weight, fruit weight, cavity size ratio, and the color values on the Hunter L a b scale. The Hunter values were transformed to CIELab values (appendix A). The

resultant L*, a* and b* values were then utilized to calculate chroma and hue which are more appropriate characters for statistical analyses (McGuire, 1992). The cavity size ratio was calculated by dividing the cavity diameter by the fruit diameter.

Means and standard deviations for each trait were calculated for all crosses using Quattro Pro 4.0.. These provided an idea of the dispersion of individual tree values within each cross. These statistics along with the data appear in appendix B. It was readily apparent that extensive variability existed within crosses for the majority of traits examined.

ANOVA

To measure the significance of the differences among crosses, analyses of variance were performed for each individual trait. Each ANOVA contained three replications of each cross corresponding to the three blocks sampled in the diallel. The number of trees per cross sampled in each replication (including reciprocals) ranged from three to eight. Crosses were the treatments. The first cross, 157 x 180 was missing in each instance, so only 27 rather than 30 entries were present.

Correlation analyses were also carried out to observe relationships in the behaviour of certain traits. Correlations between the expression of eight traits were calculated using Minitab 8.2.

Combining Ability Methods

General and specific combining abilities for the five parents and their crosses were calculated from the progeny means alone. Parent data was not available from the diallel. The fixed model was chosen for several reasons. The parents are themselves the population under study and are not a random sample from a population in Hardy Weinberg equilibrium (Griffing, 1956; Gardner and Eberhart, 1966). Also, epistatic interactions are likely given the extremely heterozygous genetic base. Gardner and Eberhart method III without parents and Griffing's method IV were both utilized in the analyses for the sake of comparison. The combining ability results were identical for both methods.

Combining Abilities Model

The model for the analyses is:

$$C_{ij} = \mu + g_i + g_j + S_{ij}$$

The grand mean is represented by μ, while g_i and g_j are the general combining abilities for the two parents involved in the cross and S_{ij} is the specific combining ability for the cross. The GCA represents an average performance of a parent in its hybrid offspring. The SCA evinces cases where particular progeny deviate from expected

performance (Christie et al.,1988). This expected performance can be calculated by adding the grand mean to the two GCA values from the parents involved in the cross (Simmonds, 1979). The difference between this value and the observed value of the trait for a cross is the SCA for that cross (Figure 1).

The mean for the missing cross, 180 x 157 was estimated from the averages of the other crosses involving these two parents. The missing datum had to be calculated for each trait evaluated. All calculations were carried out using Quattro Pro.

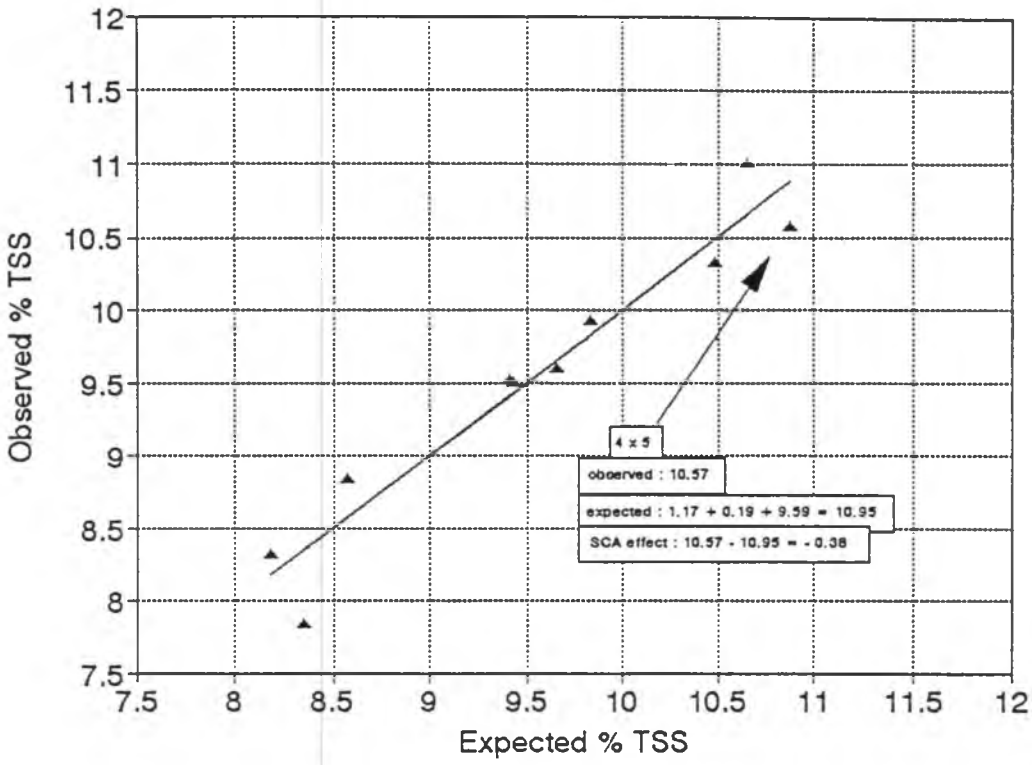


FIGURE 1. SCA FOR TSS FROM REGRESSION OF OBSERVED ON EXPECTED VALUES

CHAPTER 3
RESULTS

Guava Isozyme Evaluation

Parent Verification

The results of isozyme phenotype scoring confirmed the suspicion that many labels on parental trees were incorrect. All three trees labeled 'Allahabad' had identical zymotypes and fruit characters corresponding to this variety. The sole HKP tree also exhibited fruit with the described characteristics of the variety.

However, trees labeled R x S, KHK, 180 and 157 exhibited numerous zymotypes, indicating that they were not clonal material (Table 2). Three of the four R x S trees were identical, and fit the previous descriptions of this variety, but a fourth tree had a distinct zymotype. The isozyme phenotypes for this tree indicated that it was probably a seedling of 'Beaumont'.

All three acid varieties expressed several zymotypes. The majority of trees labeled KHK were identical and exhibited the varietal characteristics. However, a few trees had variant zymotypes. In contrast, trees labeled 157 and 180 expressed an assortment of zymotypes and fruit characters. The original descriptions of these varieties and zymotypes of some original trees from Dr. Nakasone's research were used to distinguish actual clones

TABLE 2. ISOZYME PHENOTYPES FOR FIVE PARENTS AND MISLABELED CLONES.

	Isozymes						
Clones	ACO	ALD	IDH	LAP-2	MDH	PGI	PGM
180^{t}	FF	SN	FF	FF	SS	FF	FM
157^{t}	FF	NN	FS	FS	FS	FF	FF
R x S^{t}	FS	SN	FS	FF	FS	FS	FF
Allahabad^{t}	FF	SN	SS	FF	FF	FF	FF
HKP^{t}	FS	SS	FS	FF	SS	FS	FF
180^{w}	SS	SS	FF	FF	SS	SS	FF
180^{w}	SS	SS	FF	SS	SS	FF	MS
157^{w}	SS	SS	FF	SS	SS	FS	MS
157^{w}	SS	SS	FF	SS	SS	FF	--
666	SS	SS	FF	FS	SS	FS	MS

t - true clone

w - wrong genotype

ACO = aconitase; IDH = isocitrate dehydrogenase; LAP = leucine amino-peptidase; MDH = malate dehydrogenase; PGI = phosphoglucoisomerase; PGM = phosphoglucomutase

F = fast; S = slow; M = medium; N = null

from unselected seedlings. Parental trees were relabeled and a record of the zymotypes kept for future reference.

Hybrid Progeny Verification

The analyses of parental zymotypes indicated that the progenies in the diallel may also have been mixed up. To determine the extent of the problem, each of the 435 trees under evaluation was analyzed electrophoretically for variation in six to eight different isozyme systems. This extensive examination of the progeny zymotypes was carried out to identify trees having the expected zymotypes based on the true parents. This included tallying the segregation ratios of the progeny for alleles at the different isozyme loci. Table 3 provides the chi-square values which support the assumption of Mendelian segregation for five isozymes.

The results revealed an unfortunate situation. Less than half of the crosses were progeny of both correct parents. The final tally revealed that 14 out of 34 crosses were correct for all three replications. Crosses were either incorrect or correct over all the replications, as seed from a single fruit was used to plant each cross.

The degree of contamination for KHK and R x S was predominantly due to the precocious flowering of the incorrectly labeled trees during the period when the crosses were made. The

TABLE 3. ISOZYME SEGREGATION IN PROGENY FROM FIVE GUAVA PARENTS AND CHI-SQUARE VALUES.[a]

			Expected			Observed				
Enz.	Cross[b]	n	SS	FS	FF	SS	FS	FF	X	P > X
PGI	1 x 3	125	0	62.5	62.5	0	62	63	0.008	0.99 ns
	1 x 1	48	0	0	48	0	0	48		
	3 x 3	34	8.5	17	8.5	11	20	3	6.183	0.10 ns
IDH	1 x 3	36	0	18	18	0	16	20	0.444	0.50 ns
	2 x 3	35	17.5	17.5	0	12	23	0	3.457	0.10 ns
	1 x 2	31	0	31	0	0	31	0		
MDH	1 x 3	24	0	12	12	0	14	10	0.666	0.50 ns
	2 x 3	34	17	17	0	16	18	0	0.117	0.90 ns
	1 x 2	60	0	60	0	0	60	0		
LAP	1 x 3	102	0	51	51	0	49	53	0.156	0.90 ns
	1 x 1	93	0	0	93	0	0	93		
Enz.	Cross	n	SS	NS	NN	SS	NS	NN		
ALD	4 x 5	17	0	8.5	8.5	0	11	6	1.471	0.10 ns
	2 x 5	26	13	13	0	12	14	0	0.154	0.90 ns
	4 x 2	22	0	22	0	0	22	0		

a - parents: 180, 157, 666, Hong Kong Pink, Allahabad Safeda

b - involves several crosses with the same genotypes at the locus in question: 1 = FF, 2 = SS, 3 = FS, 4 = NN, 5 = NS.

157 and 180 crosses exhibited a mixture of zymotypes reflecting the numerous different genotypes labeled as the same clone.

Due to the extensive isozyme characterization of the trees, the actual parentage for each cross was known and invalid crosses could be eliminated. From the data set of 250 trees evaluated in the fall 1992-winter 1993 season, 137 were found to be useful hybrids. The parent, KHK, was dropped from subsequent analyses because only one of the crosses involving it was correct. The five remaining parents were the focus of subsequent statistical evaluations.

The parent labeled R x S was originally chosen for the diallel as a sweet pink-fleshed guava with *Mucor* rot resistance (Ito et al., 1976). Although isozyme analyses revealed that this parent was not R x S, it was nonetheless retained in the diallel as seedling 666, because it had been used consistently as a parent in all the crosses.

Among the ten possible intercrosses of these five parents, nine were represented. The cross of 157 and 180 was not true. However, numerous reciprocals were legitimate and were bulked together to increase the number of progeny for evaluation. The likelihood of significant reciprocal differences was considered less important than the bolstering of statistical analyses with a larger number of crosses and trees per cross.

Diallel

Cross Performance

The results of the ANOVA's determine whether or not diallel analyses are valid. Only when significant differences between crosses were revealed were combining abilities calculated. Among the eight traits examined, all but two exhibited significant differences between crosses (Table 4). Fruit weight and cavity size ratio were not significantly different between crosses. TSS, % acid, % seed weight, L*, and chroma all exhibited highly significant differences between crosses.

The coefficients of variation in Table 5 indicate the degree of experimental error associated with the ANOVA's for each trait. High CV values were identified for % acid and hue. Much lower values were observed for TSS, lightness and chroma. Percent seed had an intermediate CV value of 17.6.

Extensive variation between crosses was expected for TSS, % acid, % seed weight and color. These traits were highly variable among the parents. Figure 2 demonstrates this with a regression of TSS on % acid for 137 individuals. After confirming the significance of variation between crosses, the diallel analyses were carried out.

TABLE 4. CROSS MEANS AND SIGNIFICANCE FOR EIGHT TRAITS

	Trait means							
Cross	TSS	% Acid	% Seed	L*	Chrom	Hue	Weight	CSR
1x2	9.501	1.262	3.042	44.22	22.76	0.702	134.40	0.694
1x3	8.317	0.956	1.973	44.16	22.49	0.705	81.17	0.675
1x4	10.320	1.261	3.632	51.49	17.49	1.113	136.00	0.683
1x5	9.607	1.082	2.815	41.08	25.27	0.538	137.90	0.691
2x3	7.833	0.475	3.331	42.09	22.62	0.681	141.00	0.702
2x4	11.003	1.959	3.971	44.40	23.41	0.640	141.30	0.716
2x5	9.927	1.836	2.530	42.08	25.30	0.535	169.00	0.698
3x4	9.977	0.772	3.438	43.90	20.73	0.668	123.90	0.697
3x5	8.837	0.507	2.548	41.78	22.25	0.608	113.70	0.731
4x5	10.565	0.578	3.170	49.19	14.70	1.002	143.90	0.703
F - test	**	**	**	**	**	*	NS	NS

* and ** significant at $P < 0.05$ and 0.01, respectively.

NS - not significant at $P < 0.1$.

TSS = % total soluble solids; CSR = cavity size ratio; L* = lightness.

Parents: 1 = 180; 2 = 157; 3 = 666; 4 = Allahabad Safeda; 5 = Hong Kong

TABLE 5. ANALYSIS OF VARIANCE MEAN SQUARES FOR SIX TRAITS.[a]

		Trait Mean Squares					
Source	df	TSS	%Acid	% Seed	Lightness	Chroma	Hue
Reps	2	0.042	0.306*	0.438	10.760	18.370**	0.053
Cross	8	3.382**	11.830**	1.188**	38.300**	36.700**	0.122*
Error	16	0.424	0.077	0.286	7.021	2.583	0.047
Total	26						
CV		6.79	26.50	17.60	5.96	7.45	30.10

* and ** significant at $P < 0.05$ and 0.01 respectively

CV = coefficient of variation

a - based on nine crosses including 137 F1 plants

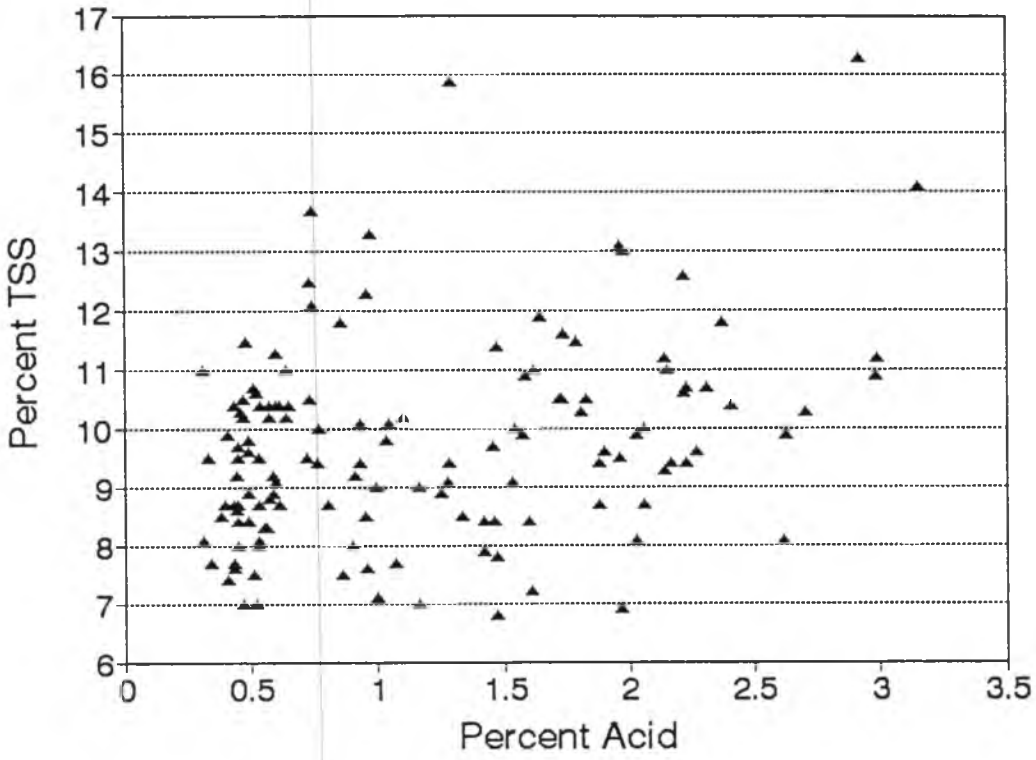


FIGURE 2. RELATIONSHIP BETWEEN TSS AND ACID

GCA and SCA Values

Certain parents and cross combinations exhibited desirable combining ability results. 'Allahabad' possessed the highest GCA for TSS, % seed, lightness component of color (L*), and hue (Table 6). The GCA values for % acid and chroma were highest in 157. The parent 666 had low GCA values for all traits but chroma.

Table 7 summarizes the SCA values for all six traits. Among the crosses, 'Allahabad' x 'HKP' exhibited the lowest SCA values for chroma and % acid. The cross, 157 x 666, had the lowest SCA value for TSS, while 180 x 666 was lowest for % seed weight. The 180 x 'Allahabad' cross possessed the lowest SCA values for lightness and hue color components. High SCA values for TSS were apparent in the crosses, 666 x 'Allahabad,' and 157 x 'Allahabad.' The crosses involving 157 with 'Allahabad' and HKP exhibited high SCA values for % acid. The highest SCA values for % seed weight were those for 180 x HKP and 157 x 666.

The diallel ANOVA results and ratios of GCA to SCA were combined in Table 8. Levels of significance for F were determined as well. GCA variance was highly significant for total soluble solids, % acid and chroma. The SCA variance was significant for acid and chroma. In all six traits, the GCA to SCA variance ratios were greater than one. They ranged from 1.4:1 for hue to 12.1:1 for soluble solids.

TABLE 6. GENERAL COMBINING ABILITIES FOR SIX TRAITS

Parents	TSS	% Acid	% Seed Weight	Lightness	Chroma	Hue
180	- 0.203	0.095	- 0.239	1.061	- 0.400	0.061
157	- 0.030	0.419	0.231	- 1.657	2.427	- 0.106
666	- 1.130	- 0.522	- 0.297	- 1.941	0.428	- 0.072
Allahabad	1.170	0.098	0.677	3.745	- 3.491	0.182
HKP	0.194	- 0.091	- 0.372	- 1.208	0.236	- 0.065
Grand mean	9.589	1.069	3.045	44.439	21.702	0.719

TABLE 7. SPECIFIC COMBINING ABILITIES FOR SIX TRAITS

Cross	TSS	% Acid	% Seed Weight	Lightness	Chroma	Hue
1 x 2	0.146	- 0.320	0.005	0.373	- 1.767	0.029
1 x 3	0.062	0.314	- 0.540	0.600	- 0.043	- 0.003
1 x 4	- 0.240	0.000	0.150	2.243	- 1.120	0.152
1 x 5	0.028	0.009	0.381	- 3.216	2.929	- 0.177
2 x 3	- 0.590	- 0.490	0.351	1.246	- 1.936	0.140
2 x 4	0.275	0.373	0.018	- 2.120	2.770	- 0.155
2 x 5	0.175	0.439	- 0.370	0.504	0.933	- 0.013
3 x 4	0.348	0.127	0.012	- 2.340	2.095	- 0.162
3 x 5	0.185	0.051	0.172	0.494	- 0.116	0.025
4 x 5	- 0.390	- 0.500	- 0.180	2.218	- 3.746	0.165

Parents: 1 = 180; 2 = 157; 3 = 666; 4 = Allahabad; 5 = HKP

TABLE 8. ANALYSES OF VARIANCE OF COMBINING ABILITIES FOR SIX TRAITS

	Mean squares[a]			
Trait	GCA	SCA	Error	GCA/SCA
Total soluble solids	2.045***	0.169	0.452	12.1:1
Percent acidity	0.356***	0.208**	0.082	1.7:1
Percent seed weight	0.597	0.156	0.305	3.8:1
L* color value	17.340	6.563	7.490	2.6:1
Chroma	13.860***	8.736**	2.755	1.6:1
Hue	0.043	0.031	0.050	1.4:1

** and *** significant at $P < 0.05$ and 0.01, respectively.

a - degrees of freedom for GCA, SCA and error were 5, 4 and 15, respectively.

TABLE 9. PHENOTYPIC CORRELATIONS BETWEEN TRAITS (n=137).[a]

Trait	% Acid	% Seed	Lightness	Chroma	Hue	Fruit Wt.	Cavity Size Ratio
TSS	0.323***	0.426***	0.198*	- 0.133	- 0.181	0.002	0.129
% Acid		0.182	0.049	0.245*	0.172	0.017	0.121
% Seed			0.097	- 0.020	- 0.007	- 0.277**	0.251*
Lightness				- 0.801***	- 0.883***	0.098	- 0.063
Chroma					- 0.749***	- 0.104	0.019
Hue						- 0.250*	0.072
Fruit Wt.							- 0.069

*, ** and *** significant at $P < 0.05$, 0.01 and 0.001, respectively.

a - based on 137 F1 plants from 17 crosses involving five parents.

Correlation

In addition to the combining ability analyses, all traits were subjected to correlation tests. Data from 137 trees were input into Minitab 8.2 and each trait was correlated with every other trait. Table 9 lists the r values and their significance at three probability levels.

The correlation between total soluble solids and acidity was positive and significant at the 0.001 level while TSS/seed weight was positive and significant at the 0.01 level. The correlation between % seed weight and fruit weight was negative and significant at the 0.01 level. The three color components, lightness, chroma and hue exhibited highly significant negative correlations between each other.

Phenotypic Observations

In addition to the array of empirical data gathered, various other observations were made regarding fruit quality. These included susceptibility to thrips, rot and fruit flies. Also considered were fruit shape, flavor, texture, color and aroma. In addition, comments about frequency of puffy, cracked and misshapen fruit were included. Observations for each of the progeny can be found in appendix C. Presence of severe red banded thrip and fruit

fly damage as well as rot was very common. Few of the progeny exhibited high quality for a majority of characteristics.

CHAPTER 4
DISCUSSION

Experimental Conditions

The original intention of this experiment was to create a full diallel to evaluate six important guava clones as possible parents for a breeding program. The confusion about parent identity diminished the number of useful crosses in the diallel. Only after extensive isozyme evaluation of trees did it become obvious that the only possible approach would be a half diallel. In order to collect sufficient data representing every cross, reciprocals were combined in every instance. This ignored the possibility of reciprocal differences and may have reduced the significance of the variance between crosses for various traits. However, it was the only hope of evaluating the parents in a diallel.

The other serious deficiency of the data was the complete abscence of the 180 x 157 cross. This presented an obstacle to calculating combining abilities and their variances. Means for this cross were calculated from the average of the averages of the two parents in their other crosses. This value was not included in the ANOVA's. Consequently the degrees of freedom for treatments was reduced to eight in the initial ANOVA (Table 5).

The combining ability ANOVA includes degrees of freedom for all the crosses. To compensate for the inclusion of the missing mean datum, one degree of freedom was removed from the error to

reduce significance. GCA degrees of freedom was four as five parents were evaluated. SCA degrees of freedom was five corresponding to ten possible crosses less the five parents.

Sources of Variation

Table 4 illustrates the existence of significant differences in variation between crosses for the six traits examined. The high levels of variation in the characters within crosses corresponds to the extensive heterozygosity in the parents. All six traits are also subject to environmental influence. This is apparent in Table 1 as well.

Temperature, water stress, soil erosion and insect damage were variable throughout the blocks in the field. These factors undoubtedly contributed to error by modifying expression of the traits in varying degrees. The lack of significant differences in fruit weight between crosses is a good example of the environment limiting genetic expression. Poor irrigation, tree crowding and soil erosion put stress on the trees, preventing them from developing maximum fruit size.

Fruit size seems to be limited severely by these adverse conditions. This was evident from comparison of the limited data collected in the spring to the extensive data from the fall harvest. The environmental conditions, predominantly rainfall, were much better in the first season. The fruit size was also much larger. In

addition, for the limited number of trees examined from both seasons, TSS and acidity were higher during the first.

Coefficients of Variance

The CV values in Table 5 suggest that for the traits % acid and hue, high levels of experimental error were present. Numerous extreme deviations from the mean and a correspondingly flatter distribution curve reveal such a situation. This detracts from the value given to significant differences between crosses. Assumptions about the variance estimates and thus combining abilities may not accurately reflect actual additive and epistatic genetic variance. The other traits, particularly TSS, exhibited desirably small CV values. The variance estimates for these traits are more sound statistics. Combining abilities calculated for these traits are better representatives of genetic variance.

Variance Estimates

Components of variance and heritabilities were not calculated as they are not available from the fixed model (Hallauer, 1988; Christie, 1988). It would not be legitimate to extrapolate results of this experiment to other guava clones not included. The GCA and SCA results do, however, provide meaningful estimates for the contribution to particular traits by each parent. The significance of GCA mean square indicates that additive genetic transmission is

important. Significance of SCA mean square suggests that dominance and epistatic interaction effects contribute to expression of the trait (Baker, 1978).

Total Soluble Solids

This trait is very important for both processing and fresh fruit quality. Its tendency to fluctuate has been a limiting factor in many varieties. The high GCA to SCA variance ratio from Table 8 suggests that among these five parents, the primary genetic contributions are additive affects. Upon examination of the individual GCA estimates, it becomes evident that 'Allahabad' is by far the best contributor of high TSS levels to the progeny. HKP is second, while 180, 157 and 666 are the least effective in transmitting this trait. These values are logical, considering that 'Allahabad' and HKP both express higher TSS levels than the other parents.

Deviations from the levels predicted by the GCA's are evident in the SCA's. The single largest deviation from the performance predicted by GCA's was in the cross 157 x 666 (Table 7). The SCA's for 180 x 'Allahabad' and 'Allahabad' x HKP also exhibit large negative deviations from expected performance. These SCA's indicate the involvement of dominant and epistatic genetic effects which confound the results of the more predictable additive genetic effects. Positive deviations from predicted performance are relatively large for 157 x 'Allahabad' and 666 x 'Allahabad'. These values indicate the possibility of hybrid vigor. If any of these

progeny are superior to both parents with regards to TSS levels, then transgressive variation comes into play.

Percent Acidity

This trait is also quite variable in the parents. Like TSS, it is considered to be quite important. Consistently high levels for processing and low levels for fresh fruit are required. The GCA to SCA variance ratio is not large (Table 8). Additive effects are most likely not as predominant in determining % acid as would be preferred by the breeder. The positive GCA values belong to 157, 180 and 'Allahabad'. Selection 157 is by far the highest, and thus transmits the greatest degree of acid to its progeny. This might be expected knowing that this parent exhibits the highest % acidity of all the clones. In contrast, 180, also a highly acidic variety, has a relatively low GCA, indicating that it may not contribute as much acidity to the progeny as might be assumed. GCA's for 'Allahabad' and 'HKP' are both close to zero, indicating that these varieties do not contribute much acidity to their progeny. The very low GCA value of 666 suggests that this variety contributes much less to the acidity of its progeny than the other parents.

SCA values are quite variable. There are numerous departures from the levels of acidity predicted by GCA's. The crosses 180 x 157, 157 x 666 and 'Allahabad' x HKP all had relatively large, negative SCA's. These crosses all exhibited substantially less acid than would be predicted by the GCA's of the parents. The 157 x

'Allahabad' and 157 x HKP crosses exhibited higher levels of acid than would be predicted, as indicated by their large, positive SCA's. The degree of departure of many crosses from the predicted performance indicated by the high SCA's in relation to GCA's suggests the importance of dominant and epistatic genetic effects for this trait. The acidity level is not likely to be easily predicted in crosses involving these parents. However, 157 appears to transmit this trait more additively than the other parents.

Percent Seed Weight

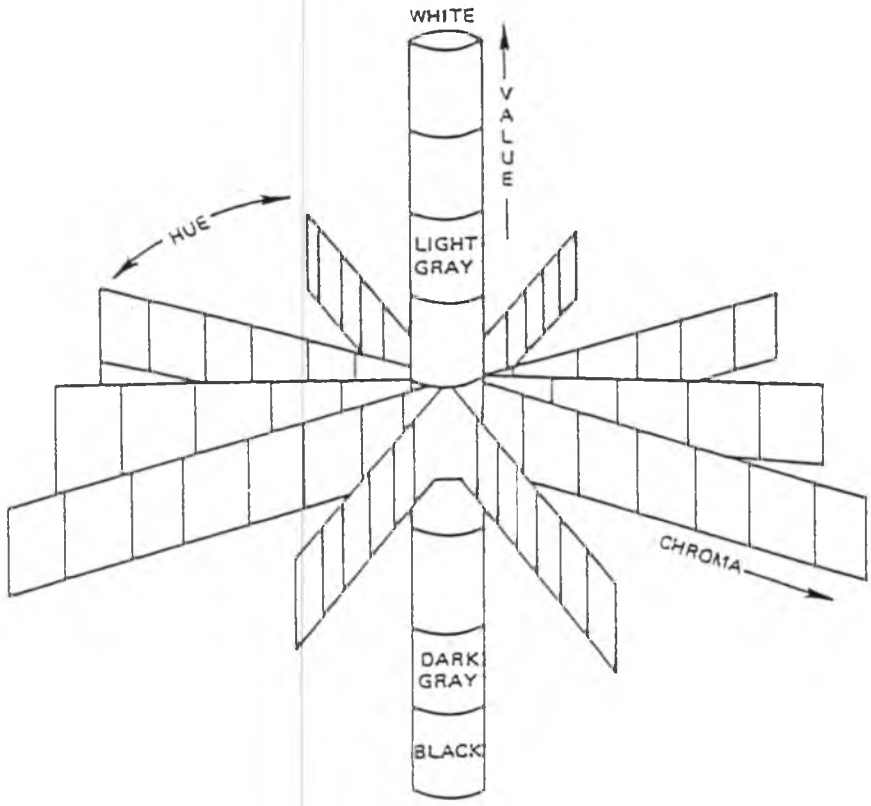
This trait affects palatibility of the fresh fruit as well as degree of wastage for processors. Many people considered the reduction of seeds to be the highest priority for guava improvement. The GCA to SCA variance ratio is relatively high. The contribution of additive genetic affects to this trait is likely to be high. Table 6 reveals that 'Allahabad' and 157 contribute high degrees of seed weight to their progeny. HKP, 666 and 180 transmit very small effects to this trait. Because less seed weight is desirable, lower GCA's correspond to superior parents, for this trait.

Major negative deviations from predicted performance are evident in 180 x 666, 157 x HKP and 'Allahabad' x HKP (Table 7). These are actually desirable departures because they represent a reduction in seed weight. Positive departures from GCA predictions are visible in 157 x 666 and 180 x HKP. These indicate greater seed weights than predicted by GCA. Seed weight is controlled by a

multitude of genetic factors, and both additive and dominance effects are likely to contribute to expression of this trait. However, from the results, it appears that HKP is the best parent for contributing to low seed weight, and its effect in the progeny is predictable.

Color Components

L* value describes the lightness or value of the color. It ranges from black (L*=0), to white (L=100). It incorporates reflectance and modifies the hue. Lightness is measured on an axis perpendicular to the rectangular plane of hues describing the different colors (Figure 3). Chroma is the measure of color saturation or intensity and is quantified by the value of the hypotenuse of the right triangle formed by the A* and B* coordinates (Appendix D). The hue values are expressed in radians or degrees and describe the angle created by the A* and B* values, as coordinates on the color plane. The hue angle reveals the color. The majority of hue values for guava puree correspond to angles between 0 and 40 in quadrant I and 0 and -40 in quadrant III (Table 4). This is due to the predominance of red and pink fruit types. The higher chroma values correspond to more intense hues. The greatest proportion of L* values are near 50, indicating that most hues are neither dark nor light, but grayish.



The Munsell Color System. Hues are spaced around the vertical lightness axis called "value." There is an increase in saturation (chroma) with horizontal distance from the central axis to the outside of the color solid.

FIGURE 3. THREE DIMENSIONAL COLOR SYSTEM[a]

a - from Hunter (1987)

Lightness

The GCA to SCA ratio for L* is 2.6:1. This suggests that additive genetic effects contribute more than dominance or epistatic effects to the trait. 'Allahabad' and 180 exhibit positive GCA's, indicating that they are good contributors for high L* values in an additive manner. This is not surprising since they have the lightest colored fruit. In contrast, the other parents are poor contributors to high L* values as evinced by their negative GCA's. These parents all have dark pink fruit.

SCA values reveal numerous departures from expected performance. 180 x HKP, 157 x 'Allahabad' and 666 x 'Allahabad' all exhibited substantial negative deviations from L* values predicted by the GCA's. This indicates the presence of darker than expected phenotypes. Lighter than expected phenotypes are also common, as indicated by the positive deviations in all the other crosses. The role of dominance genetic effects is highly likely in determining color. This has been proposed by Subramanyam (1992), and would explain the large SCA values. However, it is also possible that not all aspects of color are controlled by qualitative traits, explaining some of the high GCA's and apparent additive effects. The extensive range of lightness and intensity observed in guava may be due to the interaction of numerous genes, and thus quantitatively inherited.

Chroma

The chroma GCA to SCA ratio, 1.6:1, was not very large. The likelihood that additive effects predominate over dominance effects is probably low. GCA's indicate that 157, 666 and HKP contribute the most to high color intensity. The high value for 157 suggests that it is the best transmitter of this effect. The crosses involving this parent, however all exhibit deviations from expected values. Combined with 666 it is highly negative, but with 'Allahabad', highly positive. Similar scenarios are evident with the other parents. The role of dominance effects appears to be important for this trait.

Hue

Hue refers to color, and the qualitative nature of this trait has already been proposed (Subramanyam, 1990). The low GCA to SCA variance ratio, 1.4:1, implies that dominance effects can be important contributors to expression of color. All the GCA's are low. 'Allahabad' has the highest GCA, indicating that it is the strongest contributor to higher hue values. These values are in radians. Higher values relative to the other parents translate to less red and more yellow. The fact that 'Allahabad' is the only non-pink parent explains this phenomenon.

Correlation of Traits

The correlation analyses provided some interesting results (Table 9). The highly significant positive correlation between TSS and % acid is the most exciting observation. This indicates that numerous progeny produced fruit with high levels of soluble solids and high levels of acid. This can be visualized by regressing values for these two traits onto one another to produce a scatter diagram (Figure 2) It suggests that these two traits can complement each other in expression. The prescence of high TSS and acid levels is very desirable for processing guavas. Both sugar and acid are added to processed guava products. These represent serious expenses for the processor. Higher levels in the fruit translates to reduced costs and improved profits.

A less desirable correlation is that between TSS and seed weight. The significant value indicates that numerous progeny exhibit a greater percentage of seeds in combination with a high TSS level. The significant correlation between chroma and acid indicates that light saturation may be higher in fruits with greater acidity. The significant correlation between seed weight and hue suggests that for these progeny, a higher percentage of seed weight corresponds to a color beyond red and pink and towards white-yellow. The fact that the single white parent, 'Allahabad,' also exhibited high seed weight lends support to this observation. It would be interesting to evaluate possible linkage between color and seed weight as attempted by Subramanyam (1990).

CHAPTER 5
CONCLUSIONS

Reliability of Data

The results of the diallel analyses are valuable because they represent the first attempt in Hawaii to quantify the expression of various desirable traits in guava. In fact, this experiment is the only example found of diallel analysis for guava. However, several insurmountable problems arose during the course of the experiment.

The confusion of parentage was identified, but it drastically reduced the data set and changed the approach to statistical analyses. The inclusion of reciprocals decreased the error in the variance analyses, increasing significance for differences between crosses. Adjustment of degrees of freedom can compensate for some of the added significance.

The replications reduce the error due to environment, but severe conditions in the field during the experiment obviously affected all trees. Water stress and thrips caused excessive damage to many trees and their fruit. The death of several progeny from apparent drought stress indicated the severity of the problem.

Russetting, cracking and puffiness in many fruit obscured the true expression of the progeny phenotype in many instances. Every effort was made to evaluate healthy fruit, because the extremely poor environmental conditions were definitely not representative of any commercial guava orchard.

Utility of Results

Taking all setbacks in stride, an extensive data set was collected and did reveal useful information about the parents and their contributions to various traits in the progeny. The following results should be valuable to further guava breeding efforts in Hawaii:

1. The most promising result of the diallel analysis was the apparent additive transmission of the genes controlling TSS levels in these parents.
2. It appears that 'Allahabad' and HKP are good contributors to high TSS levels and should be included in the breeding program.
3. HKP and 180 have the advantage of being good contributors to low percent seed weight.
4. To increase percent acidity, it would be advisable to include 157 as a parent. This clone appears to be effective at contributing to high acidity.
5. Selection 157 is also the best transmitter for the characteristic of low hue value. This corresponds to a darker pink or red color, which is preferred in Hawaii.

It is risky to extrapolate from these results to predict the behaviour of other useful guava clones. However, since no other evaluations have been carried out here, the present experiment

provides the only basis for predicting transmission of the traits from parent to offspring.

It may save much time to select desirable guava parents which express the traits exhibiting high GCA/SCA ratios in a similar fashion to the best additive combiners from this experiment. Clones with high TSS, like 'Allahabad,' or low % seed weight, like HKP, could be included in the breeding program with the assumption that they will contribute these traits in an additive fashion to their progeny. This approach ignores the limitations of the fixed model, but it may be successful while saving time, money and a lot of labor by the breeder.

In addition to the diallel results, this experiment also provided some apparently desirable hybrids which may be useful not only in continuing the breeding program but for quality trials as well.

Future Breeding Strategies

The identification of additively transmitted traits is a benefit to the breeding program. The parent clones already possess many superior characteristics. The ability to predict the contribution to desirable traits such as TSS by these parents in their progeny will expedite the process of developing superior hybrid guavas.

The collection of guava germplasm in Hawaii is one of the best in the world. The availability of many good varieties will provide the foundation for a serious breeding program. A complete diallel including a larger number of good clones would be a practical next

step. This will allow more robust statistical analyses. In addition to combining abilities, heritabilities and heterosis values can be calculated (Gardner and Eberhart, 1966). Inbreeding depression can be studied and the possibility of developing inbred clones evaluated. These goals can be accomplished only if the available resources and expertise are organized. The future for guava should depend on the effort made here in Hawaii.

APPENDIX A
COLOR CONVERSION FORMULAS

Conversion of Hunter L a b to CIE L* a* b* values using X, Y, Z scale (Hunter, 1987).

CIE L* a* b*

$L^* = 116(Y/Yo)^{(1/3)}-16$

$a^* = 500[(X/Xo)^{(1/3)}-(Y/Yo)^{(1/3)}]$

$b^* = 200[(Y/Yo)^{(1/3)}-(Z/Zo)^{(1/3)}]$

Hunter L a b

$L = 100(Y/Yo)^{(1/2)}$

$$a = \frac{Ka(X/Xo-Y/Yo)}{(Y/Yo)^{(1/2)}}$$

$$b = \frac{Kb(Y/Yo-Z/Zo)}{(Y/Yo)^{(1/2)}}$$

$X = 0.98041(0.01L^2+aL/Ka)$

$Y = 0.01L^2$

$Z = 1.18103(0.01L^2-bL/Kb)$

Illuminant C

Xo = 98.041
Yo = 100.0
Zo = 118.103
Ka = 175
Kb = 70

$Chroma = (a^{*2} + b^{*2})^{1/2}$

$Hue = ArcTangent(b^*/a^*)$

APPENDIX B
TREE MEANS AND STANDARD DEVIATIONS

BLK	X	ROW	TREE	TSS	%ACID	SD WT	AVG WT	STD	CSR	STD
A	323	5	13	7.7	1.07	1.04	81.08	15.26	0.57	0.71
A	323	5	16	7.6	0.43	2.80	117.34	20.84	0.61	0.54
B	323	5	7	7.5	0.86	0.64	64.86	17.03	0.69	0.64
B	323	5	8	7.8	1.47	0.73	62.51	9.50	0.69	0.72
C	323	6	5	10.6	0.52	2.11	90.81	23.53	0.68	0.67
C	323	6	7	8.3	0.56	2.88	70.43	10.14	0.73	0.50
A	325	1	17	13.7	0.74	5.90	175.79	40.74	0.66	0.53
A	325	1	18	10.5	1.72	7.02	187.35	18.71	0.69	0.96
A	325	1	19	10.7	2.23	6.31	188.79	34.94	0.72	0.74
B	325	2	9	10.4	0.57	5.03	127.31	15.03	0.65	0.62
C	325	1	10	8.7	0.61	4.48	121.83	16.03	0.69	0.66
C	325	1	12	10.9	1.58	2.36	71.78	11.05	0.65	0.78
A	326	1	1	9	0.99	4.46	142.08	22.23	0.67	0.97
A	326	2	2	9.4	2.23	3.08	156.90	26.15	0.61	1.32
A	326	2	3	10.2	0.57	2.70	115.43	8.95	0.61	1.18
A	326	2	4	9.4	1.88	3.87	197.13	30.60	0.59	1.36
A	326	7	6	8.5	0.95	3.73	169.87	32.86	1.16	1.04
A	326	7	7	9.4	1.28	2.35	133.24	16.30	0.67	0.73
A	326	7	8	10.5	0.73	2.93	121.83	24.61	0.65	0.38
B	326	2	21	9.4	0.76	5.00	110.96	32.04	0.75	0.55
B	326	2	23	11.8	0.85	3.34	89.24	21.82	0.66	0.70
B	326	7	12	8.7	0.80	3.01	129.65	15.71	0.63	0.64
C	326	3	20	9.2	0.44	4.02	130.00	32.86	0.74	0.65
C	326	5	6	10.5	1.73	3.96	180.50	15.41	0.69	1.00
C	326	5	7	8.4	1.46	4.24	156.20	18.58	0.63	0.58
A	329	4	17	10.4	2.41	3.49	103.19	11.07	0.76	1.12
A	329	4	18	9.7	1.45	3.89	123.16	16.31	0.72	1.11
A	329	4	20	8.1	2.62	3.29	106.13	24.23	0.78	0.94
B	329	1	1	7	1.16	2.38	135.00	18.92	0.60	0.80
B	329	1	2	7.2	1.61	3.64	135.66	14.75	0.66	0.78
B	329	1	3	6.9	1.97	2.56	179.13	21.68	0.67	1.04

BLK	X	ROW	TREE	TSS	%ACID	SD WT	AVG WT	STD	CSR	STD
B	329	1	4	7.6	0.96	2.70	181.38	15.94	0.59	1.16
C	329	1	17	8	0.90	3.25	110.96	21.24	0.71	0.65
C	329	1	18	7.9	1.42	2.40	94.45	24.03	0.71	0.71
C	329	1	20	11.9	1.64	1.95	69.01	24.49	0.75	0.89
A	334	3	22	10	2.06	4.19	89.41	4.93	0.72	2.07
A	334	3	23	13.1	1.96	4.63	119.93	17.80	0.71	0.92
A	334	3	24	13	1.98	5.17	144.80	32.54	0.69	1.00
B	334	6	1	11.4	1.47	4.27	122.08	9.83	0.76	2.43
B	334	6	4	10.5	1.83	6.35	180.01	26.58	0.72	0.72
C	334	6	21	8.1	2.03	7.19	120.24	25.54	0.71	0.64
C	334	6	22	14.1	3.15	5.15	107.86	27.31	0.71	0.34
C	334	6	23	10	1.54	8.03	214.33	42.55	0.74	0.88
C	334	6	24	9.9	1.57	5.39	99.03	15.14	0.72	0.68
A	335	6	17	9.6	1.90	1.88	151.81	48.39	0.64	0.89
A	335	6	18	11	1.62	4.50	179.83	33.88	0.70	1.97
A	335	6	19	9.3	2.14	4.40	136.79	34.93	0.73	0.99
A	335	6	20	8.5	1.33	1.68	142.51	42.23	0.67	0.87
B	335	3	1	11.8	2.37	4.68	134.22	32.10	0.73	0.82
B	335	3	3	11.2	2.99	5.07	175.04	64.07	0.72	0.61
B	335	3	4	8.7	2.06	3.04	143.24	21.17	0.66	1.99
C	335	1	15	9.1	1.27	4.47	185.33	22.25	0.65	1.44
C	335	1	16	9.5	1.96	5.68	221.73	20.02	0.67	0.81
A	338	3	6	7.1	1.00	1.76	143.28	22.00	0.60	1.07
A	339	5	5	9.2	0.91	2.99	135.03	17.73	0.64	0.75
A	339	5	6	8	0.45	2.03	78.19	12.88	0.73	0.85
A	339	5	8	6.8	1.47	4.03	130.06	12.49	0.64	1.22
C	339	2	9	8	0.53	1.55	83.51	22.15	0.68	0.84
C	339	2	11	11.6	1.74	1.00	86.50	9.89	0.69	0.73
C	339	2	12	8.9	1.25	1.78	58.01	8.73	0.77	1.15
A	340	6	8	7.6	0.43	5.09	206.69	26.27	0.64	0.89
C	340	1	8	7	0.52	3.16	75.28	8.91	0.76	0.80
A	343	1	9	9.5	0.72	6.06	122.60	4.40	0.67	2.37
A	343	1	10	9.2	0.59	4.11	99.43	18.35	0.66	0.37
A	343	1	11	9.1	1.53	4.27	146.68	25.15	0.68	1.03
B	343	5	17	7.7	0.43	5.30	146.31	19.39	0.67	0.53
B	343	5	18	7.5	0.51	4.06	105.68	10.79	0.73	0.99

BLK	X	ROW	TREE	TSS	%ACID	SD WT	AVG WT	STD	CSR	STD
B	343	5	19	11.2	2.14	4.82	74.95	5.65	0.71	0.68
B	343	5	20	7	0.47	4.14	131.84	22.93	0.69	0.60
C	343	5	23	8.6	0.44	3.48	127.20	22.72	0.67	0.54
C	343	5	24	13.3	0.97	5.10	135.00	13.77	0.77	0.72
A	344	2	13	9.6	0.49	3.36	144.74	28.51	0.67	0.72
A	344	2	14	8.9	0.49	2.81	145.39	29.78	0.65	0.64
A	344	2	16	10.5	0.47	4.58	117.49	22.04	0.72	0.90
B	344	4	1	9.4	0.93	4.63	120.70	27.21	0.68	0.71
B	344	4	2	8.9	0.59	3.83	114.53	14.74	0.76	0.95
B	344	4	3	10	0.77	5.00	98.20	27.56	0.77	1.63
B	344	4	4	7.7	0.34	2.79	121.78	26.00	0.70	0.67
C	344	3	21	8.7	0.43	3.30	90.86	24.08	0.75	0.81
C	344	3	22	9.5	0.45	4.10	110.40	12.22	0.78	0.86
C	344	3	23	10.4	0.65	3.96	112.79	9.59	0.80	1.00
C	344	3	24	8.7	0.53	2.76	51.95	7.79	0.73	0.92
A	357	6	21	11	2.15	2.65	81.32	24.67	0.72	0.62
A	357	6	24	10.7	2.31	5.10	92.00		0.76	
B	357	4	9	10.3	2.71	4.90	185.80	37.76	0.80	0.14
B	357	4	10	9.1	0.60	2.70	105.93	20.06	0.65	0.56
B	357	4	11	10.6	0.52	2.04	106.68	37.11	0.62	0.65
B	357	4	12	9.2	0.44	3.20	78.13	10.45	0.69	0.90
C	357	2	17	8.5	0.38	9.26	244.38	34.62	0.68	0.97
C	357	2	18	9.6	2.27	6.01	143.28	30.91	0.67	0.56
C	357	2	20	10.2	0.47	5.12	167.16	15.95	0.66	1.80
A	358	5	9	9.4	2.17	4.40	176.90	72.32	0.70	0.82
A	358	5	10	8.7	1.88	7.15	169.51	19.04	0.72	1.19
A	358	5	11	10.6	2.22	5.80	137.80	8.94	0.77	1.00
A	358	5	12	16.3	2.92	3.55	77.45	7.00	0.68	1.00
C	358	3	9	8.4	1.42	4.76	139.19	25.15	0.65	0.75
C	358	3	10	12.6	2.22	8.65	217.95	36.07	0.72	0.75
C	358	3	11	9.9	2.63	5.53	127.40	31.76	0.71	0.68
A	359	7	1	8.7	0.45	4.63	167.91	19.64	0.63	0.56
A	359	7	4	10.1	0.93	5.10	189.38	51.25	0.68	0.46
B	359	7	13	9.8	1.03	3.73	176.00	9.40	0.66	0.29
B	359	7	14	11.5	0.48	3.58	119.85	33.87	0.67	0.57
B	359	7	15	10.4	0.54	6.83	192.56	24.46	0.67	0.74

BLK	X	ROW	TREE	TSS	%ACID	SD WT	AVG WT	STD	CSR	STD
B	359	7	16	12.1	0.74	5.73	146.99	13.00	0.66	0.92
A	362	4	9	9.7	0.45	5.93	213.74	26.69	0.69	0.46
A	362	4	10	9.8	0.49	6.43	219.43	33.19	0.71	0.62
A	362	4	11	9.9	0.41	3.86	127.44	32.78	0.70	0.66
A	362	4	12	10.4	0.60	4.15	221.79	25.43	0.68	0.54
B	362	6	14	12.3	0.96	4.67	80.86	22.90	0.74	0.82
B	362	6	15	10.3	0.46	4.81	181.00	26.73	0.71	0.96
B	362	6	16	12.5	0.73	7.20	186.43	7.57	0.80	0.76
C	362	5	9	11	0.31	1.61	92.43	14.20	0.64	0.45
C	362	5	10	15.9	1.29	3.50	41.05	6.75	0.67	1.20
C	362	5	11	8.4	0.45	2.78	105.41	13.99	0.69	0.62
C	362	5	12	8.1	0.31	2.51	107.73	17.16	0.67	0.67
A	367	3	17	11.5	1.79	3.70	187.70	32.45	0.69	0.99
A	367	3	18	10.2	1.10	3.03	165.81	42.47	0.68	0.78
A	367	3	20	10.1	1.04	3.50	117.10	24.21	0.69	0.83
B	367	3	17	10.9	2.98	4.53	143.64	29.67	0.79	0.70
B	367	3	20	9	1.16	4.65	196.56	14.85	0.67	0.84
C	367	4	13	10.3	1.81	4.00	130.77	10.37	0.70	1.50
C	367	4	14	9.9	2.03	3.87	158.19	36.18	0.74	1.18
C	367	4	15	8.4	1.60	3.53	121.46	17.74	0.72	0.74
A	368	5	1	7.4	0.41	1.00	116.51	20.32	0.65	1.17
A	368	5	2	8.1	0.53	4.10	159.25	11.48	0.72	0.82
A	368	5	4	8.3	0.55	2.44	153.80	19.87	0.67	0.95
B	368	6	21	8.7	0.40	2.31	96.10	6.62	0.78	0.97
C	368	4	21	8.4	0.49	0.98	120.60	28.49	0.75	0.49
A	370	2	17	10.2	0.64	4.80	246.41	62.55	0.72	0.88
A	370	2	18	11	0.64	5.30	157.85	35.38	0.72	0.52
B	370	4	13	8.8	0.57	6.78	196.26	25.52	0.64	0.64
B	370	4	14	9.5	0.33	5.10	149.83	13.25	0.74	1.16
B	370	4	15	10.4	0.61	5.03	170.46	55.31	0.76	0.87
B	370	4	16	10.4	0.43	5.20	174.51	23.91	0.73	0.84
C	370	3	13	11.3	0.60	5.38	175.08	27.64	0.70	0.65
C	370	3	14	10.7	0.51	4.40	191.40	32.51	0.67	0.90
C	370	3	15	9.5	0.53	5.25	213.08	46.37	0.68	0.60

BLK	X	ROW	TREE	SD/FRT	L*	A*	B*	Chroma	Hue
A	323	5	13	0.01	46.21	16.38	13.79	16.29	0.61
A	323	5	16	0.02	44.43	15.66	13.32	15.40	0.61
B	323	5	7	0.01	44.76	16.80	16.60	17.32	0.67
B	323	5	8	0.01	43.07	16.80	11.89	15.59	0.53
C	323	6	5	0.02	42.21	22.45	16.43	20.96	0.52
C	323	6	7	0.04	43.79	18.98	15.27	18.29	0.57
A	325	1	17	0.03	57.83	-2.62	13.30	10.25	-1.36
A	325	1	18	0.04	61.65	-2.18	13.27	10.48	-1.39
A	325	1	19	0.03	59.91	-1.28	14.47	11.03	-1.47
B	325	2	9	0.04	41.91	17.22	13.73	16.29	0.57
C	325	1	10	0.04	44.23	18.94	16.08	18.57	0.59
C	325	1	12	0.03	46.17	18.35	13.52	17.64	0.54
A	326	1	1	0.03	40.11	22.27	12.43	19.51	0.42
A	326	2	2	0.02	46.42	21.91	12.46	20.18	0.44
A	326	2	3	0.02	39.45	20.49	12.94	18.14	0.47
A	326	2	4	0.02	39.14	22.79	11.24	19.51	0.38
A	326	7	6	0.02	41.59	20.53	10.61	17.92	0.40
A	326	7	7	0.02	39.97	21.12	11.75	18.42	0.42
A	326	7	8	0.02	40.85	22.00	13.91	19.76	0.46
B	326	2	21	0.05	39.10	23.24	13.84	20.43	0.44
B	326	2	23	0.04	41.24	16.02	12.21	14.89	0.56
B	326	7	12	0.02	41.59	21.40	14.12	19.46	0.48
C	326	3	20	0.03	39.26	21.51	12.53	18.80	0.44
C	326	5	6	0.02	43.94	23.36	14.77	21.54	0.46
C	326	5	7	0.03	41.20	24.90	12.29	21.79	0.37
A	329	4	17	0.03	48.10	17.97	15.86	18.39	0.62
A	329	4	18	0.03	44.97	21.28	15.64	20.31	0.53
A	329	4	20	0.03	46.41	11.36	13.98	13.12	0.80
B	329	1	1	0.02	44.86	21.22	13.72	19.72	0.48
B	329	1	2	0.03	44.92	18.36	13.48	17.47	0.54
B	329	1	3	0.01	43.91	19.76	14.68	18.72	0.54
B	329	1	4	0.01	42.81	21.48	14.27	19.75	0.49
C	329	1	17	0.03	43.14	20.27	15.59	19.24	0.55
C	329	1	18	0.03	43.37	22.16	16.55	20.97	0.53
C	329	1	20	0.03	44.14	18.03	15.80	17.82	0.61
A	334	3	22	0.05	48.74	15.31	13.57	15.78	0.64

BLK	X	ROW	TREE	SD/FRT	L*	A*	B*	Chroma	Hue
A	334	3	23	0.04	41.59	20.02	13.62	18.28	0.50
A	334	3	24	0.04	45.63	15.64	13.89	15.73	0.63
B	334	6	1	0.03	41.91	17.70	14.89	16.97	0.59
B	334	6	4	0.04	45.46	18.44	13.38	17.57	0.54
C	334	6	21	0.06	42.41	23.98	13.88	21.58	0.43
C	334	6	22	0.05	46.47	16.89	15.33	17.21	0.64
C	334	6	23	0.04	41.35	18.38	13.30	16.92	0.53
C	334	6	24	0.05	40.88	24.48	16.88	22.42	0.48
A	335	6	17	0.01	44.40	20.39	12.71	18.73	0.47
A	335	6	18	0.03	44.68	22.05	16.67	21.14	0.53
A	335	6	19	0.03	43.29	22.61	14.24	20.71	0.46
A	335	6	20	0.01	39.96	19.07	12.47	17.02	0.49
B	335	3	1	0.03	44.23	18.76	13.55	17.68	0.53
B	335	3	3	0.03	42.97	22.79	15.42	21.10	0.49
B	335	3	4	0.02	45.16	21.56	12.00	19.60	0.43
C	335	1	15	0.02	39.63	21.68	13.30	19.16	0.45
C	335	1	16	0.03	41.47	23.37	14.18	21.00	0.45
A	338	3	6	0.01	42.58	17.05	11.81	15.69	0.52
A	339	5	5	0.02	44.11	14.04	11.01	13.46	0.59
A	339	5	6	0.03	43.07	16.46	16.28	16.73	0.67
A	339	5	8	0.03	47.40	14.38	15.33	15.64	0.72
C	339	2	9	0.02	41.74	19.78	15.66	18.67	0.56
C	339	2	11	0.01	45.19	18.60	13.79	17.78	0.54
C	339	2	12	0.03	44.78	14.10	16.78	15.64	0.76
A	340	6	8	0.02	41.57	17.75	13.72	16.62	0.56
C	340	1	8	0.04	42.61	17.40	14.75	16.82	0.60
A	343	1	9	0.05	44.65	15.15	9.81	13.94	0.51
A	343	1	10	0.04	44.32	16.37	10.85	15.12	0.51
A	343	1	11	0.03	40.54	19.85	11.54	17.46	0.44
B	343	5	17	0.04	44.25	18.84	12.73	17.52	0.51
B	343	5	18	0.04	42.94	16.95	12.48	15.86	0.55
B	343	5	19	0.06	48.24	13.21	14.92	14.84	0.75
B	343	5	20	0.03	43.74	18.55	13.86	17.55	0.55
C	343	5	23	0.03	42.63	18.54	12.37	16.97	0.50
C	343	5	24	0.04	40.08	17.44	13.60	16.15	0.56
A	344	2	13	0.02	41.23	19.87	11.38	17.54	0.44

BLK	X	ROW	TREE	SD/FRT	L*	A*	B*	Chroma	Hue
A	344	2	14	0.02	39.93	19.28	10.38	16.65	0.42
A	344	2	16	0.04	40.64	18.76	12.61	16.92	0.50
B	344	4	1	0.04	45.51	14.59	11.94	14.32	0.60
B	344	4	2	0.03	40.92	18.78	12.53	16.95	0.50
B	344	4	3	0.05	46.98	7.63	14.40	11.47	1.01
B	344	4	4	0.02	40.29	21.20	13.18	18.87	0.46
C	344	3	21	0.04	41.99	19.72	15.26	18.56	0.55
C	344	3	22	0.04	40.71	21.92	14.70	19.87	0.48
C	344	3	23	0.04	39.76	23.07	15.89	20.88	0.49
C	344	3	24	0.05	41.44	16.85	14.37	16.16	0.60
A	357	6	21	0.03	57.30	-4.42	14.18	11.17	-1.24
A	357	6	24	0.06	60.76	-4.63	13.17	10.89	-1.20
B	357	4	9	0.03	49.80	14.26	10.55	14.07	0.57
B	357	4	10	0.03	59.78	-2.63	11.70	9.34	-1.33
B	357	4	11	0.02	60.50	-3.07	10.78	8.85	-1.27
B	357	4	12	0.04	43.57	19.67	13.94	18.39	0.52
C	357	2	17	0.04	40.59	21.51	12.66	19.03	0.44
C	357	2	18	0.04	46.23	21.48	13.93	20.19	0.48
C	357	2	20	0.03	59.51	-3.65	13.37	10.65	-1.23
A	358	5	9	0.02	45.15	19.71	11.56	18.00	0.45
A	358	5	10	0.04	44.93	19.25	11.90	17.70	0.47
A	358	5	11	0.04	47.58	19.03	14.17	18.55	0.55
A	358	5	12	0.05	44.97	17.79	16.44	17.98	0.63
C	358	3	9	0.03	43.21	21.50	14.31	19.84	0.49
C	358	3	10	0.04	46.32	15.52	14.12	15.82	0.64
C	358	3	11	0.04	46.05	22.08	12.35	20.23	0.43
A	359	7	1	0.03	45.08	18.03	12.94	17.08	0.53
A	359	7	4	0.03	38.92	23.55	12.42	20.34	0.40
B	359	7	13	0.02	42.30	18.93	11.86	17.08	0.48
B	359	7	14	0.03	41.95	19.50	12.56	17.65	0.48
B	359	7	15	0.04	59.21	-3.99	12.45	10.11	-1.24
B	359	7	16	0.04	57.91	-4.62	13.97	11.15	-1.22
A	362	4	9	0.03	57.69	-4.71	11.56	9.64	-1.16
A	362	4	10	0.03	58.06	-3.26	9.18	7.66	-1.21
A	362	4	11	0.03	39.82	15.99	9.13	13.83	0.45
A	362	4	12	0.02	57.38	-5.36	12.12	10.18	-1.12

BLK	X	ROW	TREE	SD/FRT	L*	A*	B*	Chroma	Hue
B	362	6	14	0.06	58.00	-3.56	14.15	11.00	-1.30
B	362	6	15	0.03	58.59	-1.90	9.61	7.67	-1.36
B	362	6	16	0.04	40.62	18.54	13.87	17.10	0.54
C	362	5	9	0.02	61.95	-2.66	15.26	11.92	-1.38
C	362	5	10	0.09	43.80	19.44	18.28	19.52	0.63
C	362	5	11	0.03	58.47	-3.57	12.75	10.14	-1.27
C	362	5	12	0.02	42.44	21.10	9.99	18.36	0.38
A	367	3	17	0.02	41.57	17.61	13.79	16.54	0.56
A	367	3	18	0.02	40.54	18.66	11.99	16.66	0.48
A	367	3	20	0.03	39.47	20.88	11.51	18.10	0.42
B	367	3	17	0.03	45.25	22.12	13.67	20.48	0.46
B	367	3	20	0.02	38.61	28.60	12.33	24.48	0.32
C	367	4	13	0.03	42.16	20.48	14.10	18.83	0.50
C	367	4	14	0.02	42.27	22.89	13.08	20.49	0.43
C	367	4	15	0.03	42.04	17.41	10.77	15.60	0.48
A	368	5	1	0.01	42.68	18.52	10.69	16.51	0.45
A	368	5	2	0.03	41.74	18.57	13.80	17.26	0.54
A	368	5	4	0.02	42.99	16.22	12.47	15.34	0.57
B	368	6	21	0.02	40.99	19.37	12.02	17.28	0.47
C	368	4	21	0.01	42.18	17.11	12.49	15.88	0.54
A	370	2	17	0.02	55.19	-4.62	11.71	9.51	-1.17
A	370	2	18	0.03	39.04	22.98	11.90	19.79	0.39
B	370	4	13	0.03	57.80	-2.75	12.83	9.96	-1.34
B	370	4	14	0.03	38.79	22.16	13.15	19.37	0.44
B	370	4	15	0.03	55.25	-3.32	11.02	8.71	-1.26
B	370	4	16	0.03	39.80	21.49	11.14	18.55	0.40
C	370	3	13	0.03	40.31	19.65	12.92	17.62	0.49
C	370	3	14	0.02	41.30	18.32	10.24	16.06	0.44
C	370	3	15	0.02	41.95	16.32	10.94	14.82	0.51

CROSS	ROW	TREE	COLOR	SIZE	TEXTURE	AROMA	FLAVOR
323	A5	13	PINK	SM	SOFT	GOOD	OK
323	A5	16	PINK	MED	MED	OK	OK
323	B5	5	PINK	SM	SOFT	POOR	POOR
323	B5	7	PINK	SM	SOFT	OK	OK
323	B5	8	PINK	SM	SOFT	GOOD/BERRY	OK
325	A1	17	WHITE	MED-LG	SOFT	POOR	OK/MUSKY
325	A1	18	WHITE	LG	SOFT	POOR	POOR/SOUR
325	A1	19	WHITE	LG	MED	POOR/MUSKY	POOR/SOUR
325	B2	9	PINK	MED	MED	OK	OK
325	C1	10	LT. PINK	MED	MED	GOOD	GOOD
325	C1	12	PINK	SM	SOFT	OK	OK
326	A2	1	PINK	MED	MED	OK	OK
326	A2	2	DK. PINK	MED	FIRM	VGOOD	GOOD/BERRY
326	A2	3	DK. PINK	MED	MED	OK	OK
326	A2	4	DK. PINK	LG	MED	OK	OK/BERRY
326	A7	6	PINK	MED-LG	FIRM	VGOOD	GOOD
326	A7	7	DK. PINK	SM-MED	FIRM	GOOD	VGOOD/TANGY
326	A7	8	DK PINK	SM-MED	SOFT	GOOD	GOOD
326	B2	21	DK. PINK	SM-MED	SOFT	GOOD/BERRY	GOOD
326	B2	22	PINK	MED-LG	SOFT	POOR	POOR
326	B2	23	PINK	SM-MED	SOFT	POOR	POOR
326	B7	12	DK. PINK	MED	FIRM	GOOD	GOOD
326	C5	6	DK. PINK	MED	MED	POOR/ONION	OK

CROSS	ROW	TREE	COLOR	SIZE	TEXTURE	AROMA	FLAVOR
334	A3	21	PINK	MED-LG	SOFT	GOOD/BERRY	GOOD
334	A3	22	PINK	SM-MED	MED	VGOOD	GOOD/TANGY
334	A3	23	DK. PINK	MED	MED	GOOD/BERRY	GOOD/TANGY
334	A3	24	PINK	MED	MED	GOOD/BERRY	GOOD/TANGY
334	B6	1	DK. PINK	MED	MED	OK	OK
334	B6	4	DK. PINK	MED-LG	MED	GOOD	OK
334	C6	21	DK. PINK	SM-LG	SOFT	GOOD	OK
334	C6	22	PINK	SM	SOFT	POOR	POOR
334	C6	23	PINK	MED-XLG	FIRM	GOOD	GOOD
335	A6	17	RED	SM-LG	MED	GOOD	OK
335	A6	18	RED	LG	FIRM	GOOD	VGOOD/TANGY
335	A6	19	DK. PINK	SM-LG	MED	OK	OK
335	A6	20	DK. PINK	MED	SOFT	OK	POOR
335	B3	1	PINK	SM-LG	MED	OK	OK
335	B3	3	PINK	SM-LG	MED	POOR	OK
335	B3	4	DK. PINK	SM-LG	MED	GOOD/BERRY	GOOD/TANGY
335	C1	15	DK. PINK	LG	MED	OK	OK
335	C1	16	DK. PINK	LG	MED	POOR	OK
339	A5	5	DK. PINK	SM-MED	MED	GOOD/BERRY	OK
339	A5	6	PINK	SM-MED	MED	OK/MUSKY	OK
339	A5	7	PINK	MED	SOFT	GOOD	GOOD
339	A5	8	LT. PINK	MED	MED	OK	OK
339	C2	9	PINK	SM-MED	SOFT	OK	GOOD

CROSS	ROW	TREE	COLOR	SIZE	TEXTURE	AROMA	FLAVOR
339	C2	11	PINK	SM-MED	SOFT	OK	OK
340	A6	8	PINK	MED-VLG	SOFT	GOOD/BERRY	OK
340	C1	8	PINK	SM	SOFT	OK	OK
343	A1	9	PINK	SMALL	HIGH	GOOD	GOOD/SWEET
343	A1	10	PINK	SM-MED	HIGH	GOOD	STRAWBERRY
343	A1	11	PINK	MED-LG	SOFT	OK	OK/SOUR
343	B5	17	PINK	MED-LG	MED	GOOD	GOOD
343	B5	18	LT. PINK	SM-MED	SOFT	OK	OK
343	B5	19	LT. PINK	SM.	SOFT	POOR	POOR
343	B5	20	PINK	MED-LG	MED	OK	OK
343	C5	23	LT. PINK	SM-MED	SOFT	OK	OK
344	A2	13	PINK	MED-LG	SOFT	OK	OK
344	A2	14	PINK	MED-LG	MED	OK	OK
344	A2	16	PINK	MED-LG	SOFT	OK	OK
344	B4	1	PINK	SM-MD	SOFT	OK	OK
344	B4	2	PINK	SM-MED	MED	OK	GOOD
344	B4	3	PINK	SM-LG	MED	OK	OK
344	B4	4	PINK	SM-MED	VSOFT	OK	OK
344	C3	21	PINK	SM-MED	SOFT	GOOD	OK
344	C3	22	PINK	MED	SOFT	GOOD	OK
344	C3	23	PINK	SM-MED	SOFT	OK	OK
357	A6	21	WHITE	SM-MED	MED	POOR	POOR
357	A6	22	WHITE	SM	MED	POOR	POOR

CROSS	ROW	TREE	COLOR	SIZE	TEXTURE	AROMA	FLAVOR
357	B4	9	PINK	MED-LG	FIRM	GOOD/BERRY	GOOD/TANGY
357	B4	10	WHITE	SM-MED	MED	OK	OK
357	B4	11	WHITE	SM-MED	FIRM	VPOOR	OK
357	B4	12	PINK	SM	SOFT	GOOD/STRAW	OK
358	A5	9	PINK	SM-LG	MED	OK	OK
358	A5	10	DK. PINK	MED-LG	SOFT	GOOD	GOOD/TANGY
358	A5	11	PINK	MED	MED	VGOOD/BERRY	VGOOD/TANGY
358	C3	10	PINK	LG	FIRM	GOOD	GOOD
359	A7	1	PINK	LG	MED	ODD	GOOD
359	A7	2	PINK	SM	SOFT	POOR	POOR
359	A7	3	DK. PINK	SM-MED	FIRM	POOR	GOOD
359	A7	4	DK. PINK	MED-LG	FIRM	POOR/MUSKY	POOR
359	B7	14	PINK	MED-LG	MED	GOOD	OK
359	B7	15	WHITE	LARGE	FIRM	OK	GOOD
359	B7	16	WHITE	LG	FIRM	OK	OK
359	C5	16	PINK	SM-MED	MED	OK	OK
362	A4	9	WHITE	LG	FIRM	OK	OK/MUSKY
362	A4	10	WHITE	LG	FIRM	OK	OK/MUSKY
362	A4	11	PINK	MED-LG	FIRM	OK	GOOD/TANGY
362	A4	12	WHITE	LG	FIRM	OK	OK/MUSKY
362	B6	15	WHITE	MED-LG	FIRM	POOR	OK
362	B6	16	PINK	LG	FIRM	OK	GOOD
362	C5	9	WHITE	SM-MED	FIRM	POOR	OK

CROSS	ROW	TREE	COLOR	SIZE	TEXTURE	AROMA	FLAVOR
367	A3	17	DK. PINK	MED	MED	GOOD/BERRY	GOOD/TANGY
367	A3	18	DK. PINK-R	SM-LG	MED	GOOD/BERRY	GOOD/TANGY
367	A3	20	PINK	MED	SOFT	OK	GOOD/TANGY
367	B3	17	DK. PINK	MED-LG	MED	GOOD/BERRY	GOOD/TANGY
367	B3	20	RED	LG	FIRM	VGOOD	GOOD/TANGY
367	C4	13	DK. PINK	MED	SOFT	GOOD/BERRY	OK
367	C4	14	DK. PINK	MED-LG	MED	GOOD	GOOD
367	C4	15	DK. PINK	MED	MED	VGOOD	GOOD
368	A5	1	PINK	MED	MED	GOOD	GOOD
368	A5	2	PINK	MED-LG	SOFT	GOOD/BERRY	OK
368	B6	21	PINK	SM-MED	SOFT	OK	OK
368	C4	21	PINK	MED-LG	SOFT	GOOD	OK
370	A2	17	WHITE	LG-XLG	MED	MUSKY	OK/TANGY
370	A2	18	DK. PINK	SM-LG	FIRM	POOR/MUSKY	OK
370	A2	19	PINK	MED	FIRM	POOR/MUSKY	OK
370	B4	13	WHITE	LG	FIRM	OK/SPICY	GOOD/TART
370	B4	14	PINK-RED	MED-LG	SOFT	GOOD/RASP	OK
370	B4	15	WHITE	SM-LG	MED	POOR/MUSKY	POOR
370	B4	16	PINK	MED-LG	MED	OK	OK
370	C3	16	WHITE	MED-LG	FIRM	POOR	OK

CROSS	TREE	CONSIS	RUSSET	ROT	LARVA	SHAPE	COMMENTS
323	13	THIN	MED	MED	LOW	ELLIPT	WATERSK; WHITE STRK
323	16	THICK	HIGH	VLOW	NONE	PYRI	
323	5	MED	MED	LOW	NONE	ELLIPT	
323	7	THIN	HIGH	MED	NONE	ROUND	WATERSOAK
323	8	THIN	HIGH	MED	NONE	ROUND	WATERSOAK
325	17	THICK	HIGH	MED	NONE	ELLIPT	MANY HARD SEEDS
325	18	THIN	HIGH	MED	MED	ELLIPT	JELLYLIKE LOCULES
325	19	THICK	HIGH	LOW	MED	ROUND	
325	9	MED	MED	NONE	MED	ROUND	
325	10	THICK	MED	NONE	NONE	ROUND	RIDGES
325	12	THIN	HIGH	MED	NONE	ELLIPT	WHITE STREAKS
326	1	THICK	LOW	MED	LOW	ELLIPT	WATERSOAK; RIDGES
326	2	THICK	NONE	LOW	LOW	ELLIPT	WAXY SKIN
326	3	THICK	NONE	LOW	NONE	ELLIPT	WAXY SKIN
326	4	THICK	MED	MED	NONE	PYRI	BUMBY SKIN
326	6	THICK	VLOW	LOW	NONE	PYRI	RIDGES
326	7	THICK	NONE	LOW	NONE	ELLIPT	
326	8	MED	LOW	MED	LOW	PYRI	BUMPY,BIRD DAM
326	21	MED	HIGH	MED	NONE	ELLIPT	WATERSOAK
326	22	MED	HIGH	MED	MED	ROUND	WATERSK; LG SEEDS
326	23	THIN	LOW	MED	HIGH	PYRI	
326	12	THICK	MED	LOW	NONE	ROUND	
326	6	MED	HIGH	MED	LOW	ELLIPT	BIRD DAM.

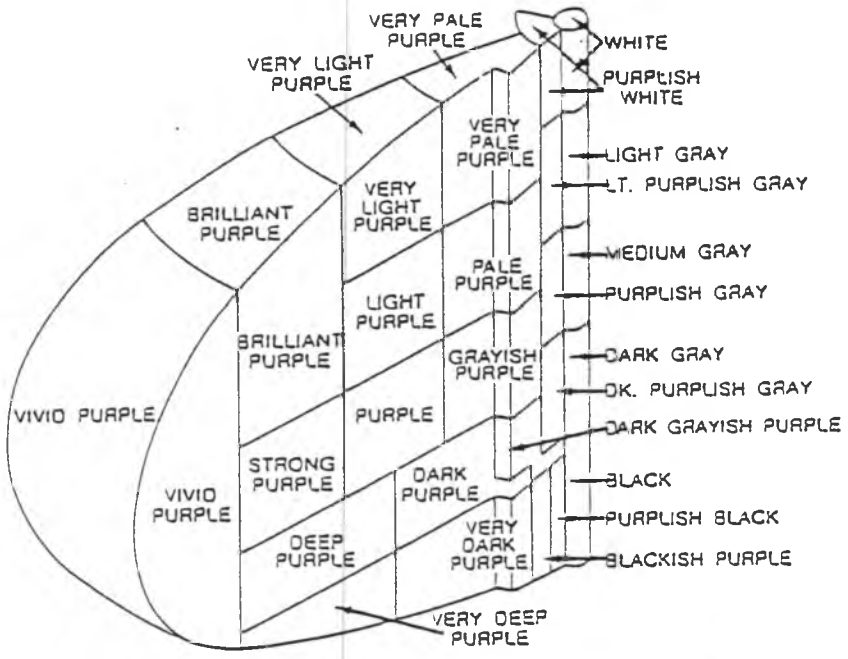
CROSS	TREE	CONSIS	RUSSET	ROT	LARVA	SHAPE	COMMENTS
334	21	THICK	MED	LOW	NONE	ELLIPT	MISSHAPEN FRUITS
334	22	THICK	HIGH	NONE	NONE	ROUND	AROMATIC
334	23	MED	HIGH	NONE	NONE	ELLIPT	XLG SEED CAVITY
334	24	THICK	HIGH	NONE	LOW	ELLIPT	
334	1	THICK	HIGH	LOW	MED	ROUND	
334	4	THICK	HIGH	LOW	NONE	ELLIPT	SOME CRACKS
334	21	MED	HIGH	LOW	NONE	ELLIPT	WATERSOAK
334	22	MED	HIGH	MED	MED	ROUND	WATERSOAK
334	23	THICK	HIGH	LOW	NONE	ELLIPT	
335	17	THICK	HIGH	LOW	HIGH	ELLIPT	WATERSK & WORMS
335	18	THICK	HIGH	LOW	NONE	ROUND	EXCELLENT
335	19	THICK	HIGH	LOW	LOW	PYRI	CRACKS; PUFFY
335	20	MED	HIGH	LOW	NONE	PYRI	PUFFY; WATERSK; BIRD
335	1	THICK	MED	LOW	LOW	ELLIPT	
335	3	MED	HIGH	LOW	MED	ELLIPT	MUCOR; BIRD DAM
335	4	MED	HIGH	LOW	NONE	ELLIPT	
335	15	THICK	HIGH	LOW	MED	ELLIPT	RIDGES; PUFFY
335	16	THICK	HIGH	NONE	NONE	ELLIPT	SALTY AROMA
339	5	THICK	MED	LOW	HIGH	ROUND	PUNGENT FLAVOR
339	6	MED	LOW	LOW	NONE	ELLIPT	PUFFY
339	7	MED	NONE	LOW	NONE	ELLIPT	
339	8	THICK	HIGH	LOW	NONE	PYRI	
339	9	MED	MED	LOW	LOW	ELLIPT	WHITE STREAKS

CROSS	TREE	CONSIS	RUSSET	ROT	LARVA	SHAPE	COMMENTS
339	11	THICK	HIGH	LOW	NONE	ELLIPT	
340	8	THICK	MED	LOW	NONE	ELLIPT	WATERSK; WHITE STRK
340	8	THIN	MED	MED	LOW	ELLIPT	
343	9	THICK	HIGH	LOW	NONE	ROUND	RADIAL RIDGES
343	10	THICK	MED	MED	NONE	ROUND	
343	11	THICK	MED	MED	MED	ELLIPT	
343	17	THICK	VLOW	NONE	NONE	ELLIPT	
343	18	THIN	LOW	MED	NONE	ELLIPT	
343	19	MED	LOW	MED	HIGH	ROUND	
343	20	MED	MED	MED	NONE	ELLIPT	PUFFY
343	23	THIN	MED	MED	NONE	ROUND	WATERSK; WHITE STRK
344	13	THICK	MED	MED	NONE	ELLIPT	
344	14	THICK	HIGH	MED	NONE	PYRI	
344	16	THICK	MED	MED	NONE	PYRI	RIDGES
344	1	MED	NONE	MED	HIGH	ROUND	WATERSOAK
344	2	THICK	HIGH	MED	NONE	ROUND	
344	3	MED	LOW	LOW	MED	ELLIPT	
344	4	MED	MED	MED	NONE	PYRI	
344	21	MED	MED	MED	NONE	ELLIPT	MISSHAPEN
344	22	THIN	MED	MED	NONE	ELLIPT	WATERSOAK
344	23	THIN	HIGH	MED	NONE	ELLIPT	MISSHAPEN; WATERSK
357	21	MED	HIGH	LOW	MED	ROUND	MALODOROUS
357	22	MED	HIGH	MED	NONE	ROUND	MALODOROUS

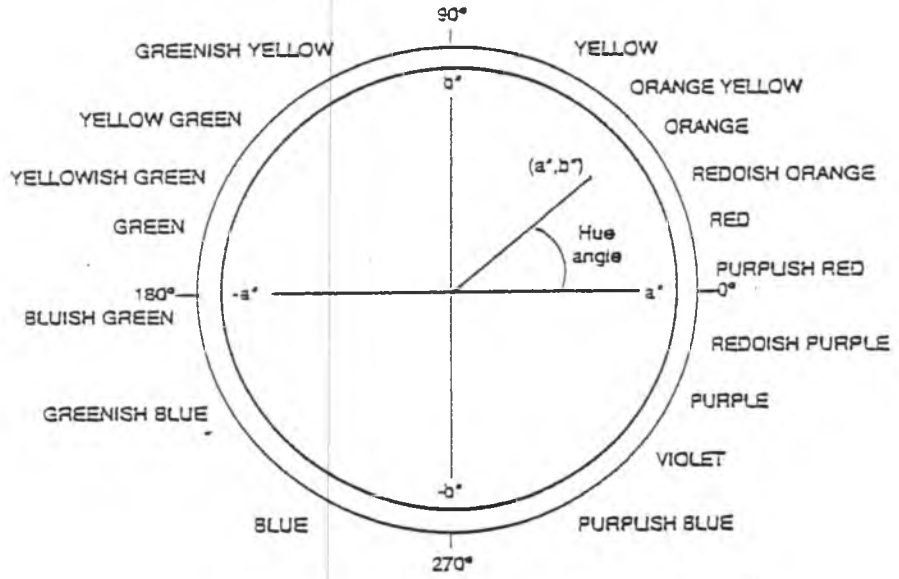
CROSS	TREE	CONSIS	RUSSET	ROT	LARVA	SHAPE	COMMENTS
357	9	THICK	MED	NONE	NONE	ELLIPT	
357	10	MED	MED	LOW	NONE	ROUND	MISSHAPEN
357	11	THICK	LOW	LOW	NONE	ROUND	MISSHAPEN; RIDGES
357	12	MED	MED	HIGH	NONE	ROUND	PUFFY
358	9	THICK	LOW	LOW	LOW	PYRI	RIDGES; BIRD DAM
358	10	MED	MED	MED	LOW	ELLIPT	WAXY; WATERSK
358	11	THICK	MED	MED	NONE	ELLIPT	MISSHAPEN; EXCELLENT
358	10	THICK	MED	MED	NONE	ELLIPT	RIDGES
359	1	MED	MED	MED	NONE	ELLIPT	
359	2	THIN	NONE	MED	MED	ROUND	
359	3	THICK	NONE	LOW	MED	ROUND	WATERSK; BIRD DAM
359	4	THICK	LOW	LOW	LOW	ROUND	
359	14	MED	MED	LOW	NONE	ELLIPT	PUFFY
359	15	THICK	LOW	LOW	NONE	ELLIPT	
359	16	THICK	LOW	LOW	NONE	ELLIPT	
359	16	MED	MED	MED	NONE	ELLIPT	MISSHAPEN
362	9	VTHICK	LOW	NONE	NONE	ELLIPT	BUMPY;BANANA FLAVOR
362	10	VTHICK	VLOW	LOW	NONE	ELLIPT	BUMPY; SOME END ROT
362	11	THICK	LOW	NONE	LOW	ELLIPT	SOME BUMPS; RIDGES
362	12	VTHICK	LOW	NONE	NONE	ELLIPT	SOME BUMPY
362	15	THICK	HIGH	LOW	NONE	ROUND	
362	16	THICK	LOW	LOW	LOW	ROUND	
362	9	THICK	LOW	LOW	NONE	ROUND	WAXY, BUMPY

CROSS	TREE	CONSIS	RUSSET	ROT	LARVA	SHAPE	COMMENTS
367	17	THICK	HIGH	NONE	NONE	PYRI	VGOOD; SOME CRACKS
367	18	THICK	HIGH	NONE	NONE	PYRI	VGOOD; RED FRUIT
367	20	MED	LOW	LOW	MED	ELLIPT	PUFFY
367	17	MED	HIGH	NONE	NONE	PYRI	WATERSK; BIRD DAM.
367	20	THICK	HIGH	LOW	NONE	ROUND	CRACKING; RIDGES
367	13	MED	HIGH	MED	MED	ELLIPT	CRACKING; WATERSK
367	14	MED	HIGH	MED	NONE	ELLIPT	
367	15	THICK	HIGH	LOW	NONE	ROUND	
368	1	THICK	NONE	MED	NONE	ROUND	ENDROT
368	2	MED	MED	MED	LOW	ELLIPT	PUFFY
368	21	MED	MED	MED	NONE	ELLIPT	
368	21	MED	HIGH	LOW	NONE	ROUND	
370	17	THICK	HIGH	NONE	NONE	ELLIPT	
370	18	THICK	MED	LOW	LOW	ELLIPT	
370	19	THICK	NONE	NONE	NONE	ROUND	WAXY; BUMPY SKIN
370	13	THICK	LOW	LOW	NONE	ROUND	
370	14	MED	HIGH	MED	NONE	ELLIPT	
370	15	THICK	HIGH	MED	NONE	ELLIPT	
370	16	THICK	LOW	LOW	NONE	ROUND	
370	16	THICK	MED	NONE	LOW	ROUND	MISSHAPEN

APPENDIX D
COLOR CLASSIFICATION



Purple segment of the color solid (Fig. 6 in Kelly and Judd, 1976).[a]



Hue sequence and hue-angle orientation on a CIELAB diagram (with ISCC-NBS color names).[a]

a - from Voss (1992)

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