INHERITANCE OF FLOWER, STEM, LEAF, AND DISEASE TRAITS IN THREE DIPLOID INTERSPECIFIC ROSE POPULATIONS

A Thesis

by

DAVID ANDREW SHUPERT

Submitted to the Office of Graduate Studies of
Texas A&M University
in partial fulfillment of the requirements for the degree of

MASTER OF SCIENCE

August 2005

Major Subject: Horticulture

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Approved by:

Co-Chairs of Committee,	David H. Byrne
	H. Brent Pemberton
Committee Members,	Javier F. Betran
	Stephen R. King
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ABSTRACT

Inheritance of Flower, Stem, Leaf, and Disease Traits

in Three Diploid Interspecific Rose Populations. (August 2005)

David Andrew Shupert, B.S., Purdue University

Co-Chairs of Advisory Committee: Dr. David H. Byrne
Dr. H. Brent Pemberton

Three F_1 plants (WOB13, WOB21, and WOB26) from the hybridization of the diploid parents *Rosa wichuraiana* 'Basye's Thornless' and 'Old Blush' (*Rosa chinensis*) were backcrossed to 'Old Blush' to produce three interspecific backcross populations to observe the segregation of several morphological and disease resistance traits.

The qualitative traits of bloom habit, flower color, flower form, and presence of stem prickles were characterized in two locations in College Station, Texas. The quantitative traits of flower size, petal size, and number of flowers per stem were measured in College Station, Texas, and number of leaflets per leaf, powdery mildew resistance, and black spot resistance were measured in College Station and Overton, Texas.

Reported modes of inheritance for flower color (pink co-dominant to white), flower form (double dominant to single), and stem prickles (prickles dominant to no prickles) agree with the results in this study. The segregation of the bloom (non-recurrent dominant to recurrent) habit trait showed a deficiency of recurrent blooming types.

Sources of variation generation and/or genotype(generation) explained most of the variation for flower size, petal sizes, flowers per stem, leaflet number, powdery mildew, and black spot resistance. Different environmental conditions within the environment made replication effects significant for flowers per stem. Low incidence level of powdery mildew and different temperatures in College Station and Overton made environment effects significant. Environment x generation and environment x genotype(generation) were significant for black spot resistance. The genetic variance is about two times greater than the environment x genetic interaction which would allow selection to be done at one environment, even though black spot resistance may change some between environments.

Additive gene action (no dominance) was observed for flower size, petal size, black spot resistance, and powdery mildew resistance. Gene action of partial dominance was observed for leaflet number. Gene action for flowers per stem could not be determined due to lack of variation.

DEDICATION

To my parents and grandparents:

who stimulated my interest in growing plants.

ACKNOWLEDGMENTS

I would like to thank my co-chairs Dr. David H. Byrne and Dr. H. Brent Pemberton for their guidance and support that helped me earn my degree. Thanks to my committee members Dr. Javier F. Betran for helping with the statistical analysis and Stephen R. King for his assistance. I would like to thank the Basye Rose Breeding and Genetics Program Group: Natalie, John, Millie, and Matt for all their help.

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CHAPTER I

INTRODUCTION

Roses are one of the most popular flowers for landscape and floriculture. However, reports of scientific research on genus *Rosa* are limited. Most of the research in scientific and trade journals has focused on physiology or cultural practices. Limited genetic research has been conducted on roses compared to other horticultural and agronomic crops. Researchers conducting genetic studies on roses have faced many challenges: incompatibility among ploidy levels, apomictic reproduction in some species of the section *Caninae*, self incompatibility, fertility barriers between species, poor germination of seeds, and the highly heterozygous nature of the genus *Rosa* (Crespel et al., 2002; Debener, 2003; Gudin, 2000; Werlemark et al., 1999).

This research will focus on the patterns of inheritance of specific morphological flower traits (bloom habit, flower color, flower form, flower size, petal size, and flowers per stem), morphological stem and leaf traits (presence of prickles on stem and number of leaflets per leaf), and disease resistance traits (powdery mildew and black spot). This research will give a foundation for better understanding of rose genetics to aid researchers and breeders of the genus *Rosa*.

This thesis has been prepared according to the style and format of HortScience.

CHAPTER II

LITERATURE REVIEW

Research in Roses

Documented genetic research in roses has been limited. Most of the research has been conducted by private growers or rose companies, who have little incentive to publish their findings (Gudin and Mouchotte, 1996). The research in older publications lacks statistics to support the results. In 1959, Stewart and Semeniuk said, "…any prediction of breeding behavior with reference to specific desirable characters is impossible…" (Stewart and Semeniuk, 1959). Since Stewart's statement there has been tremendous advancement in rose breeding. Current publications on rose genetics are focused on the inheritance of major rose traits (Debener, 1999; Gudin, 2000; Nybom et al., 1996; Rajapakse et al., 2001; Zykov and Klimenko, 1999) and the use of molecular markers or biotechnological methods in breeding (Gudin, 2000; Kaufmann et al., 2003; Rajapakse et al., 2001). Reported traits of interest include flower color, double flower form, recurrent blooming, stem prickles, petiole prickles, powdery mildew resistance, black spot resistance, male sterility, moss character, and dwarf growth habit.

Morphological Flower Traits

Bloom Habit

Plants that bloom through the whole growing season are called everblooming or recurrent blooming. Plants that bloom once during the year are called single blooming, once blooming, or non-recurrent blooming (Buck, 1960; Debener, 1999; De Vries and Dubois, 1978; Semeniuk, 1971a, 1971b). Research on recurrent blooming has shown that recurrent blooming is conditioned by a recessive allele whereas the non-recurrent blooming is conditioned by a dominant allele at one loci (Crespel et al., 2002; Debener, 1999; Debener, 2003; De Vries and Dubois, 1978; De Vries and Dubois, 1984; Rajapakse et al., 2001; Semeniuk, 1971a, 1971b; Zykov and Klimenko, 1999).

Flower Color

The pigments in rose flowers are anthocyanidins, flavonols, and carotenoids (De Vries et al., 1974). Pink flower color is caused by the accumulation of anthocyanidins in the petal cells and controlled by a major loci with white being homozygous recessive, medium pink heterozygous, and dark pink homozygous dominant for the pink allele (Debener, 1999; Debener, 2003; Lammerts, 1945b; Zykov and Klimenko, 1999). Flower pigments in petunia are conditioned by anthocyanidin genes (An2 and An6), a flavonol gene (Fl), and a hydroxylation gene (HF1) (Griesback, 2002; Wiering and De Vlaming, 1984). The genotype an2 an2 conditions white flowers and the genotype An2 _ conditions pigment formation. The intensity of the flower pigment is suggested to be conditioned by An2 interacting with other genes (Griesbach, 2002). Flower color in ornamental peaches is conditioned by multiple genes for red, pink, and white flower

color. The flower color genes are red (rr) being recessive to pink (R_), light pink (pp) being recessive to dark pink (P_), and white (ww) being recessive to color (W_) (Lammerts, 1945a).

Flower Form

In the loci for flower form, the double flower trait is controlled by a dominant allele and the single flower state is controlled by a recessive allele (Crespel et al., 2002; Debener, 1999; Debener, 2003; Lammerts, 1945b; Swim, 1948). Environmental interactions and additional minor genes are reported to influence the mean number of petals per flower (Debener, 1999; Debener, 2003; Garrod and Harris, 1974; Lammerts, 1945b; Morey, 1959; Rajapakse et al., 2001). In ornamental peaches, flower form is different than roses with the single flower form completely dominant (D_1_) to the double flower form. The number of petals in the double flower form is conditioned by Dm_1 and Dm_2 alleles (Lammerts, 1945a). Morey (1959) reported that the terminal and spring rose flowers tend to have more petals than lateral and summer flowers, that rose floral parts are arranged in whorls of five, and that most species roses have only one whorl of five petals. Morey (1959) suggests that double flowers in species roses are actually single flowers that have extra petals called petaloids. Petaloids are formed from stamen initials that fail to develop properly and make petals (Debener, 1999; Morey, 1959). In general the development of the floral organs of sepals, petals, stamens, and carpels is by three sets of functional genes A, B, and C. The combination of the A and B genes in whorl 2 designates petals and the combination of B and C genes in whorl 3 designates stamens (Honma and Goto, 2001; Tooke and Battey, 2000). Petaloids develop when the A gene

is expressed in whorl 3 which decreases the number of stamens (Tooke and Battey, 2000). Petaloids are usually smaller in size than regular petals, but at times are indistinguishable (Morey, 1959).

Flower Size

Flower size in blueberries has an additive gene action. The F_1 hybrids have flower size intermediate to the two parents (Ritzinger and Lyrene, 1999). No literature was found about the inheritance of flower size or petal size in rose.

Morphological Stem and Leaf Traits

Stem Prickles

The prickles that roses have on their stems and leaf petioles, are often referred to as thorns or bristles (Nobbs, 1984; Roberts, 1982; Rosu et al., 1995). Botanically, thorns are found at the axils of leaves and prickles are modified clusters of epidermal hairs (Rost et al., 1998). The number of prickles found on rose stems usually decrease from the bottom to the top (Andre, 2003). The presence or absence of stem prickles is controlled at one loci with the presence of prickles a dominant allele and the absence of prickles a recessive allele (Debener, 1999; Debener, 2003; Rajapakse et al., 2001). Research with blackberries, a close relative of roses, show the absence of prickles on stems is also controlled by a single recessive gene (Haskell and Hill, 1961; Pavlis and Moore, 1981; Scott and Ink, 1966). The inheritance of prickle density in roses is quantitative (Lammerts, 1945b; Swim, 1948), which has recently been reported to be controlled by two independent QTL loci (Crespel et al., 2002). Pavlis and Moore (1981) showed that prickle density in blackberry has a non additive gene action.

Leaflet Number

Rose leaflet numbers are seen as odd pinnate leaves. The leaves that are found near the shoot tip and the base of the shoot have the fewest number of leaflets with one or three. The leaves found in the middle of the shoot have the greatest number of leaflets with five to seven (Torre, 2003) and even nine to eleven. In soybeans, leaflet numbers are conditioned by two single major genes. Seven leaflet numbers in soybeans is conditioned by lf_2 and five leaflet numbers conditioned by lf_1 (Fehr, 1972). No literature was found about the inheritance of leaflet number in rose.

Diseases Resistance Traits

Powdery mildew is the major disease of greenhouse roses and is also seen in field grown roses. Black spot is the most harmful fungal disease of field grown roses (Debener, 2003; Horst, 1983; Kaufmann et al., 2003; Linde and Debener, 2003). Powdery mildew and black spot can be found in all countries where roses are grown (Alvarez, 2003; Horst, 1983; Linde and Shishkoff, 2003). Resistance to the rose pathogens powdery mildew *Podosphaera pannosa* (Wallr.: Fr.) de Bary. and black spot *Diplocarpon rosae* Wolf. are reported to be controlled by a 'gene for gene' interaction (Debener, 2003; Kaufmann et al., 2003). Races of both rose powdery mildew and rose black spot have been described (Linde and Debener, 2003; Malek and Debener, 1998).

Powdery Mildew

K. F. Wallroth first discovered powdery mildew in Germany in 1819. Powdery mildew was reported by Leveille in 1851 (Deshpande, 1980). Powdery mildew is caused by a biotrophe parasite, which lives and multiplies only on living organisms.

Powdery mildew is an ascomycete fungus *Podosphaera pannosa* (Wallr.: Fr.) de Bary., (syn. *Sphaerotheca pannosa* var. rosae (Wallr.: Fr.) Lev) (Linde and Debener, 2003). In roses, young leaves, stems, flowers, and fruit are attacked by the white powdery mildew. Symptoms of infection include leaf curling and distorted flowers. The older leaves have been observed to exhibit increased resistance to powdery mildew (Bender and Coyier, 1983; Horst, 1983; Mence and Hildebrandt, 1966). The resistance found in older leaves has been suggested to be due to increased thickness of the leaf cuticle (Conti et al., 1985; Horst, 1983). The optimum environmental conditions for powdery mildew in field grown roses are night temperature of 15.5 ^{o}C and relative humidity of 90-99% and a day temperature of 26.7 ^{o}C and relative humidity of 40-70%. Consecutive multiple cycles of these night-day conditions encourage disease development (Horst, 1983; Linde and Shishkoff, 2003).

Powdery mildew resistance is reported to be inherited as a dominant trait (Debener, 2003; Lammerts, 1945b; Linde and Debener, 2003; Swim, 1948). More recently, Linde and Debener (2003) identified eight races of powdery mildew and one resistance loci (Rpp1) (Debener, 2003). Rpp1 is an abbreviation where R stands for a dominant resistance gene in the host, pp stands for *Podosphaera pannosa*, and 1 for the first resistance gene identified (Linde and Debener, 2003). In the Linde and Debener (2003) study, they inoculated rose leaves with eight monoconidial isolates of *Podosphaera pannosa*. After incubation, the disease index was scored on whole leaf with single conidiophores. The leaves that had a disease index of 10% or more were classified as susceptible and leaves with disease index of 5% or less (with no leaves over

5%) were classified as resistant. The study showed with a ratio of 1:1 for resistance:susceptible that a single dominant resistance gene conditions resistance to race nine of *Podosphaera pannosa* (Linde and Debener, 2003).

Black Spot

Black spot is caused by the hemibiotrophic, fungus *Diplocarpon rosae* Wolf. which is able to grow on artificial media. Black spot symptoms include irregular black spots on leaves, chlorosis around the spot, and defoliation (Hamblin, 1959; Horst, 1983; Johnson, 1972). The black spots can be found on any age leaves, but are more commonly observed on lower leaves where air circulation is poor (Johnson, 1972). Favorable environmental conditions for black spot is high humidity and temperatures from 15-27 ^{o}C (Debener, 2003; Horst, 1983). The optimum time for disease development is in the autumn (Drewes, 2003).

The two black spot resistance loci (Rdr1 and Rdr2) thus far identified exhibit monogenic inheritance with resistance being dominant over susceptibility (Debener, 2003; Malek and Debener, 1998; Rajapakse et al., 2001). Rdr is an abbreviation where a R stands for a dominant resistance gene in the host, the d stands for *Diplocarpon*, the r stands for *rosae*, and the number indicates the order the resistance genes were identified (Debener, 2003; Kaufmann et al., 2003; Malek and Debener, 1998;). Malek and Debener (1998) identified five races of *Diplocarpon rosae*. In Malek and Debener (1998) study they inoculated derived generations of the tetraploid line 91/100-5 with three to five rose leaves with the race five that infects all commercial rose varieties. After incubation, the leaves were scored as susceptible if the mycelium grew beyond the

inoculated area and formed acervuli. The leaves were scored as resistant if the mycelium did not grow beyond the inoculated area. This study with the tetraploid line 91/100-5 showed segregation ratios of 35:1 in F_2 and 5:1 in BC and F_1 generations for resistance:susceptible that a single dominant gene conditions resistance to race five of *Diplocarpon rosae*. If multiple genes conditioned resistance to race five, then more generations of backcrossing would be needed to develop resistant plants (Malek and Debener, 1998).

CHAPTER III

MATERIALS AND METHODS

Plant Material

Three diploid interspecific backcross rose populations derived from a F_1 population were used to study inheritance of morphological flower traits (bloom habit, flower color, flower form, flower size, petal size, and flowers per stem), morphological stem and leaf traits (presence of prickles on stem and number of leaflets per leaf), and disease resistance traits (powdery mildew and black spot) in roses. Nineteen F_1 plants were created from the hybridization of the diploid parents *Rosa wichuraiana* 'Basye's Thornless' (BT) and *Rosa chinensis* 'Old Blush' (OB). Segregation of traits was seen in the F_1. From the nineteen F_1 plants (WOB progeny), three were selected (WOB13, WOB21, and WOB26) to backcross with 'Old Blush' producing three segregating backcross (BC) populations. There were 140, 49, and 177 plants from the BC populations OB x WOB13 (BC13), OB x WOB21 (BC21), and OB x WOB26 (BC26) respectively. The three BC populations, all nineteen F_1 plants, and the parent plants *Rosa wichuraiana* 'Basye's Thornless' and 'Old Blush' were used to characterized the segregation of morphological and disease resistance traits.

In the summer of 2003 the F_1 (WOB13, WOB21, and WOB26) were backcrossed to the other parent *Rosa wichuraiana* 'Basye's Thornless'. The BC populations had 10, 101, and 68 plants from BT x WOB13 (BT13), BT x WOB21 (BT21), and BT x WOB26 (BT26) respectively. The backcrosses to BT produced all non-recurrent blooming

plants, therefore these backcrosses were used to observe the segregation of stem prickles. In the fall of 2003, open pollinated rose hips were collected from OB and in the fall of 2004 open pollinated rose hips were collected from the three F_1 (WOB13, WOB21, and WOB26) plants. Most of the open pollinated roses are assumed to be self pollinated F_2, since not many other roses were blooming at the same time in the field. The F_2 of OB (23 plants) was observed for the segregation of the qualitative traits (bloom habit, flower form, and stem prickles). The F_2 progeny of WOB13, WOB21, and WOB26 had 110, 253, and 384 plants respectively. These were observed for the segregation of bloom habit.

Rosa wichuraiana is a diploid species rose that was introduced from east China and from Japan in the 1880's as a source for winter hardiness, disease resistance, and glabrous leaf character (Lammerts, 1945b; Swim, 1948; Wylie, 1955). *Rosa wichuraiana*, in general, and in particular the *Rosa wichuraiana* 'Basye's Thornless' used in this research is reported to be resistant to black spot (Drewes, 2003; Hamblin, 1959; Horst, 1983; Rajapakse et al., 2001; Saunders, 1970). BT has 19 to 33 mm diameter, single (5 petal) white flowers. The rose lacks prickles on the stems but has prickles on the leaf petiole. BT has a non-recurrent blooming habit, a groundcover growth, susceptibility to powdery mildew, and resistance to black spot.

The recurrent parent 'Old Blush' was first introduced as 'Old Blush China' by Peter Osbeck in 1751 in Europe. 'Old Blush' is probably many generations removed from the wild diploid species *R. chinensis* and *R. gigantea*. 'Old Blush' and similar China roses of that era were used as a source of the recurrent flowering trait in rose

development in Europe (Marriott, 2003; Wylie, 1954). OB has 38 to 72 mm diameter, double (20-30 petal) medium pink flowers. The rose has prickles on both the stems and on the leaf petiole. OB has a recurrent blooming habit, an upright bush growth and susceptibility to powdery mildew and black spot.

The F_1 WOB13 has 35-50 mm diameter, single (5 petal) light pink flower. The rose has no stem prickles but does have leaf prickles. WOB13 has a non-recurrent blooming habit, an upright trailing bush growth, and moderate resistance to powdery mildew and black spot.

The F_1 WOB21 has 30 to 40 mm diameter, single (5 petal) white flowers. The rose has prickles on both the stems and leaves. WOB21 has a non-recurrent blooming habit, an upright trailing bush growth, and moderate resistance to powdery mildew and black spot.

The F_1 WOB26 has 30 to 45 mm diameter, single (5-6 petal) light pink flower. The rose has no stem prickles but does have leaf prickles. BC26 has a non-recurrent blooming habit, an upright trailing bush growth, and moderate resistance to powdery mildew and black spot.

Environments

Three environments were used in this study. Two environments were in College Station, Texas and one environment in Overton, Texas. The first College Station location (GH) consists of raised beds behind the Texas A&M University Horticulture and Forest Science building. This location focused on the qualitative traits (bloom habit, flower color, flower form, and presences of prickles on stem) since this experimental

design had only one replication which does not allow a good estimate for quantitative analysis. GH has sandy loam soil, a top layer of bark mulch, and drip irrigation. Seedlings of each of the three BC populations were planted in the spring of 2002 in a separate bed consisting of 50 plants. The three beds each have seventeen rows (North to South orientation) with three plants per row. The seedlings were planted 4 ft apart within rows and 2 ft apart between rows. The seedlings were randomly planted within the beds with a selection emphasis placed on the recurrent blooming seedlings. The 'Old Blush', 'Basye's Thornless', and six of the WOB F_1 progeny (WOB5, WOB9, WOB13, WOB15, WOB21, and WOB26) are also in raised beds at spacing 6 ft apart.

The second environment (CS) was a field planting two miles from the Texas A&M University Horticulture and Forest Science building. All the rose traits were examined at this site. CS has sandy loam soil, weed barrier, and overhead sprinkler irrigation. CS field planting done July 2003 has four replicated blocks of 110 plants per replicate. In each replicate there were the 19 WOB F_1 progeny, 2 'Old Blush', 2 'Basye's Thornless', and about 86 random BC plants. Thirty of the random BC plants were rooted cuttings of the same BC plants in the raised beds. Each block consists of two rows 220 ft long having an East to West orientation. The seedlings and cuttings are planted 4 ft apart within the row and the rows are 15 ft apart. The experimental design was a randomized complete block for the generations (OB, BT, F_1, BC13, BC21, and BC26).

The third environment (OV) was at the Texas A&M University Agricultural Research and Experiment Center in Overton, Texas (2005). The work at this location

focused on disease resistance data and leaflet number data. OV has sandy soil and underground drip irrigation. Due to the sandy soil in this environment, fertilizer was applied in the drip irrigation. The field planting done Apr. 2004 has four replicated blocks that each contain rooted cuttings from the 19 WOB F_1 progeny, 2 'Old Blush', 2 'Basye's Thornless', and 10 BC plants from each three backcrosses. The cuttings were planted 6 ft apart within the row and the rows were 10 ft apart. This gave a total of 53 plants per replication having a North to South orientation. The experimental design was in a randomized complete block for the generations (OB, BT, F_1, BC13, BC21, and BC26).

Data Collection

Visual data was collected for the segregating traits using color standards, rating scales, and rulers as appropriate. Preliminary data was collected in the GH environment during the summer of 2002 on leaves and stems and from Mar. 2003 to Dec. 2003 on all traits. Data continued to be collected in all three environments from Mar. 2004 to Dec. 2004. The morphological and disease resistance traits were examined in the rose populations as outlined below.

Morphological Flower Traits

Bloom habit. Recurrent blooming plants produce flowers within 1 or 2 months following germination (Crespel, 2002; De Vries and Dubois, 1978). Thus recurrent blooming plants were marked as recurrent in the greenhouse the first year. After the second growing season the non-recurrent blooming plants were observed for flowering. Some of the non-recurrent blooming plants have a longer juvenile period and take

several years before flowering. Some plants including 'Basye's Thornless' were observed to set a few flowers after the first flowering of the growing season, but the plant only has one true peak flowering and is considered non-recurrent blooming.

Flower color. Flower color was assessed on recently opened flowers (within 2 days). Newly opened flowers have anthers that are bright yellow and appear moist and sticky whereas flowers that have been opened for 3 or more days have anthers that are starting to turn a dull yellowish brown color and are drying up. The plants, especially the non-recurrent blooming plants, were observed at least every other day for flowers from 15 Mar. 2004 until 24 May 2004 when the recurrent and non recurrent genotypes had flowered at least once for the year (Appendix A). From observations it appeared that the anthers changed color and dried more rapidly in warmer temperatures than under cooler conditions. Since weather and age cause flowers to change color, flower collection was done more than once on the same plant to get a mean flower color for the plant. To maintain the flowers' freshness after collection, they were collected and put into plastic bags and stored in a cooler with a cold pack. Once the flowers were inside they were characterized for flower color under normal inside light and scanned on a HP Scan Jet 5370c flatbed scanner at 200 dpi resolution. Since all of the flowers did not flower at once, the flower scans allowed comparisons of flowers in different environments and different times of flowering.

The flowers were grouped by color using the classification guidelines from the American Rose Society (2004). The flowers in the populations have shown variation from solid white/white blend, light pink, medium pink, deep pink, solid pink, and pink

blends. To determine the flower color, 'Basye's Thornless' was used as the standard for white and 'Old Blush' used as the standard for medium pink. 'Old Blush' gives a standard color of N 66 D for medium pink when using the Royal Horticultural Society color standards. Flowers from each plant were scanned on a flatbed scanner using the standard color strip N 66 D for medium pink and a ruler to measure the diameter of the flower (mm). The flower colors were grouped into three categories according to the predominant color: dark pink, pink (medium and light), and white colors for the qualitative analysis.

Flower and petal size. After the whole flower was scanned for color, the flower diameter (mm) was measured. Although a ruler was used when the flower was scanned for flower color, this measurement was not used since the flower did not always lay flat on the scanner. Since the flowers are not always perfect circles the mean of two measurements of the flower's diameter were taken. The mean of two or three flowers were measured from each plant, if the plant produced enough flowers.

Petal length from the greatest point were measured (mm) of a petal from the first whorl. The first whorl was classified as the petals farthest from the stamen and pistil. These are usually the largest petals. Two petals from each of the two or three flowers were measured as was done for flower size.

Flower form. The number of petals was counted after flower color and flower size was recorded. These counts were classified either as single flowers (less than or equal to 7 petals) or double flowers (greater than 7 petals) (Debener, 1999).

Flowers per stem. During the spring when flower color was examined the number of flowers on the pedicel was counted. The number of flowers on at least three random pedicels, if available, was recorded.

Morphological Stem and Leaf Traits

Stem prickles. During Aug. 2004, the plants were observed in the field for the presence or absence of prickles. The density of rose prickles usually decreases from the base of the plant to the top (Andre, 2003). Some plants had few stem prickles or the prickles were only at the base of the plant which made finding the prickles more difficult. The plants were observed again in Sept. 2004 to confirm the data. The backcross to BT was observed for stem prickles in Dec. 2004.

Leaflet per leaf. During the end of Sept. 2004, the stems were collected to count the number of leaflets per leaf. Stems that appeared to be mature and the internode space did not appear to be expanding anymore where collected for measurements. Two or three stems were collected from each plant and put into plastic bags and kept fresh in a cooler with an ice pack. The stems from each individual environment were all collected the same day and measurements were done in the laboratory. The number of leaflets per leaf was counted between the fifth node and seventh node. The first node was defined as the first expanding leaf at the terminal of the stem. Leaflet number was counted from the leaf found at the sixth node of the stem. The leaflet number was recorded as the closest rounded up odd number, because leaves of roses have odd number of pinnate leaflets (Torre, 2003).

Disease Resistance Traits

Resistance to pathogens can be tested by inoculating the whole plant with the pathogen (Bolton and Svejda, 1979), inoculating detached leaf with the pathogen in culture, or by observing natural infection in the field or greenhouse and by using rating scales (Bender and Coyier, 1983; Linde and Debener, 2003; Saunders, 1970), or molecular markers (Kaufmann et al., 2003). Rating scales were used to evaluate powdery mildew resistance and black spot resistance to the natural races of the pathogen present at the environments CS and OV.

In May of 2004, disease ratings were done for powdery mildew. In May, July, Aug., Sept., and Oct. of 2004 disease ratings were done for black spot (Appendix A and B). During 2004 the disease ratings were collected in two environments (CS and OV). All sides of the plants were observed when doing the ratings. The number of plants evaluated and the distance of the environments prevented collecting the disease ratings all in one day. The ratings in CS environment were not always possible to collect in one day, but all of the plants in the same replication were collected the same day. Collecting disease ratings for all environments were done as close as possible to the same day. The rating scale used for powdery mildew is as follows:

0 = No mildew is on plant

1 = One or two isolated infections

2 = Slight infection throughout plant

3 to 7 = Based on percent of leaves infected

8 = Most foliage, stems, and peduncles with infection

9 = Heavy infection throughout plant

The rating scale used for black spot is as follows:

0 = No black spot on plant

1 = One or two isolated infections

2 = Slight infection throughout plant

3 to 6 = Based on percent of leaves infected

7 = Most foliage infected except most distal

8 = All foliage infected

9 = All foliage infected, heavy defoliation, plant vigor reduced

Data Analysis

The qualitative traits were analyzed by chi-square to check the expected segregation ratios with the equation, $\chi^2 = \Sigma$ (Observed – Expected)^2 / Expected (Fairbanks and Andersen, 1999). The qualitative traits are bloom habit, flower color, flower form, and presence of stem prickles.

The quantitative traits were analyzed by analysis of variance. Analysis of variance was conducted using PROC GLM in SAS (SAS Institute, 2002). Quantitative traits were flower size, petal size, flowers per stem, number of leaflets per leaf, powdery mildew resistance, and black spot resistance. The analysis of flower traits (flower size, petal size, and flowers per stem) considered 6 generations (OB, BT, F_1, BC13, BC21, and BC26) and only the CS environment. The ANOVA model for the flower traits used the following sources of variation: replication, generation, genotype(generation), and error (Table 1). The analysis for number of leaflets per leaf, powdery mildew resistance,

and black spot resistance had the same 6 generations (OB, BT, F_1, BC13, BC21, and BC26) and two environments (College Station field CS and Overton OV). The ANOVA model used the following sources of variation: environment, replication(environment), generation, genotype(generation), environment*generation, environment*genotype(generation), and error (Table 2).

The sum of squares values from the ANOVA table allow an estimate of the phenotypic variance explained by the genotype and the environment and their statistical significance. Two times the standard error was used to determine the statistical significance among the generation means.

Gene action was determined by comparing the F_1 mean to the midparent value with the equation, midparent = [('Basye's Thornless' + 'Old Blush')/2]. The F_1 mean that is equal to the midparent value would indicate that there is no dominance (additive). Partial dominance was indicated when the F_1 mean was between the midparent value and one of the parents and a F_1 mean higher than the high parent value or lower than the low parent value indicated over dominance.

Table 1. ANOVA mean squares for flower size, petal size, and flowers per stem.

Source	df [z]	Mean squares[y]
Replication	r-1	MS_R
Generation	f-1	MS_F
Genotype (Generation)	f(g-1)	$MS_{G(F)}$
Error	(g-1)(f-1)(r-1)	MS_e
Total	rfg-1	

[z] r = number of replications, f = number of generations, g = number of genotypes.
[y] R = replication, F = generation, G = genotype, e = error.

Table 2. ANOVA mean squares for leaflet number, powdery mildew, and black spot resistance.

Source	df [z]	Mean squares[y]
Environment	e-1	MS_E
Replication (Environment)	e(r-1)	$MS_{R(E)}$
Generation	f-1	MS_F
Genotype (Generation)	f(g-1)	$MS_{G(F)}$
Environment x Generation	(e-1)(f-1)	MS_{EF}
Environment x Genotype (Generation)	(e-1)f(g-1)	$MS_{EG(F)}$
Error	e(g-1)(f-1)(r-1)	MS_e
Total	efgr-1	

[z] e = number of environments, r = number of replications, f = number of generations, g = number of genotypes.

[y] E = environment, R = replication, F = generation, G = genotype, e = error.

CHAPTER IV

RESULTS AND DISCUSSION

Qualitative Analysis

Bloom Habit

The presence of non-recurrent blooming has been reported to be conditioned by dominant gene (recessive conditions recurrent blooming) at one locus in rose (Crespel et al., 2002; Debener, 1999; Debener, 2003; De Vries and Dubois, 1978; De Vries and Dubois, 1984; Rajapakse et al., 2001; Semeniuk, 1971a, 1971b; Zykov and Klimenko, 1999). In this study, the parent 'Basye's Thornless' is non-recurrent and the other parent 'Old Blush' is recurrent. The nineteen F_1 plants all had non-recurrent blooming habit and, given the previous work on this gene, the F_1 plants should be heterozygous for the recurrent blooming gene. The expected ratio of the backcross generations crossing 'Old Blush' (homozygous recessive) to the F_1 hybrids (heterozygous) would be one non-recurrent to one recurrent plant. Surprisingly, all the BC populations had a large excess of non-recurrent progeny. The ratios seen for BC13, BC21, and BC26 were 1:10, 1:8, and 1:6 respectively with an overall ratio of 1:8.2 (Table 3).

The above results do not support the previous reports that indicate recurrent blooming is conditioned by a recessive allele whereas the non-recurrent blooming is conditioned by a dominant allele at one loci. Semeniuk (1971a) made a diploid cross with the F_1 (heterozygous) to recurrent *Rosa wichuraiana* (homozygous recessive) and had 517 plants non-recurrent and 443 plants recurrent. De Vries and Dubois (1978) and

Semeniuk (1971b) also showed that recurrent blooming was conditioned by recessive alleles in diploid, triploid, and tetraploid roses. The unexpected number of recurrent to non-recurrent blooming roses in this experiment with an overall ratio of 1:8.2 might indicate that more than one gene are involved with bloom habit in the BC populations.

Table 3. Chi square test for recurrent and non-recurrent bloom habit.

Generation[z]	Non-Rec.[y]	Recurrent	Expected Ratio	χ^2
F_1	19	0	1:0	0 ^{NS}
BC13	249	25	1:1	183.1 ***
BC21	47	6	1:1	31.7 ***
BC26	288	43	1:1	181.3 ***
BT13	10	0	1:0	0 ^{NS}
BT21	101	0	1:0	0 ^{NS}
BT26	68	0	1:0	0 ^{NS}
F_2 13	97	13	3:1	78.8 ***
F_2 21	246	7	3:1	26.3 ***
F_2 26	375	9	3:1	105.1 ***
F_2 OB	4	19	0:1	0.7 ^{NS}

[z] Abbreviations for F_1 = 'Basye's Thornless' x 'Old Blush', BC (13, 21, and 26) = 'Old Blush' x F_1 (13, 21, 26), BT (13, 21, 26) = 'Basye's Thornless' x F_1 (13, 21, 26), and F_2 (13, 21, 26, OB) = Open pollinated F_1 (13, 21, 26) and 'Old Blush'.
[y] Non-Rec. = non-recurrent.
$^{NS,*, **, ***}$ Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

A backcross from the other direction was done by the hybridization of 'Basye's Thornless' with the F_1 plants of WOB13, WOB21, and WOB26. The backcross using 'Basye's Thornless' (BT) were all non-recurrent blooming plants, which supports previous reports that recurrent blooming is conditioned by a recessive gene.

Open pollinated (mainly selfed) seeds was collected from WOB13, WOB21, and WOB26 (all heterozygous for the recessive allele) and germinated to test the expected

ratio of three non-recurrent to one recurrent plant. The ratios seen for F_2 populations do not support the expected results of three non-recurrent to one recurrent plant (Table 3). Although there is, without doubt, some outcrosses in these populations, the scarcity of recurrent types resembles the lack of recurrent types found in the OB backcross population. The ratios seen for open pollinated WOB13, WOB21, and WOB26 were 1:8, 1:36, and 1:42 respectively with an overall ratio of 1:28 (Table 3). The ratios do not fit into a recognizable pattern for one or a few genes conditioning recurrent blooming. Open pollinated 'Old Blush' have also been collected to test the expected ratio of all recurrent plants. Most of the 'Old Blush' plants are recurrent and the plants that are non-recurrent look like hybrid outcrosses having greater number of leaflets. In other hybridizations with two recurrent WOB derivatives (M2-4 and M4-4), all the seedlings from open pollinated seeds were recurrent as expected for the segregation of a homozygous recessive trait.

Research needs to be continued to determine the reason for these skewed ratios for bloom habit. One potential reason is the interspecific origin of this progeny. The plants used in this study were from an interspecific rose population whose parents belong to different botanical sections: *Synstylae* (*R. wichuraiana*) and *Chinenses* (*R. chinensis*) (Jan, et al., 1999). In the report by Semeniuk (1971 a) plants from the same botanical section *Synstylae* (*R. wichuraiana*) were used to show that recurrent blooming is conditioned by a single recessive allele. Maybe hybridizing roses from different sections influences the number of recurrent blooming plants. In the Basye Rose Breeding and Genetics Program, non-recurrent plants are one of the first plants

discarded, so the numbers of recurrent to non-recurrent have not have recorded in the past. Taking better records should help assess if the number of recurrent plants is low in other hybridizations. More hybridizations between roses from the same section and from different sections should be done to explore how interspecific crosses influence the number of recurrent blooming plants.

Another potential reason for these unexpected results could be that the homozygous recessive (recurrent) plants are weaker plants that are harder to germinate or put so much energy into producing flowers that they die at a young age giving fewer recurrent plants. This agrees with greenhouse and field observations that the recurrent blooming plants are generally smaller than the non-recurrent blooming plants.

Flower Color

The presence of dark pink flower color has been reported to be conditioned by dominant gene (heterozygous conditions light pink and homozygous recessive conditions white flower color) at one locus in rose (Debener, 1999; Debener, 2003; Lammerts, 1945b; Zykov and Klimenko, 1999). In this study, the parent 'Basye Thornless' had white flowers and the other parent 'Old Blush' had pink flowers. Segregation in the F_1 generation of pink and white flowers suggests that the 'Old Blush' parent is heterozygous for this pink color gene. The segregation of the F_1 (13 pink:6 white) fits either the 1:1 ($\chi^2 = 2.6$) or the 3 pink:1 white ($\chi^2 = 0.4$). The F_1 plants WOB13 and WOB26 had pink flowers (heterozygous). As expected the backcross with these crossed to 'Old Blush' showed a 3 pink to 1 white ratio. In addition, the pink flowers were further divided into dark pink and pink (medium and light) classes. When

the data is analyzed like this, the BC13 and BC26 progeny show a 1 dark pink:2 pink:1 white segregation indicating that the heterozygous state is expressed as a pink whereas the homozygous state is expressed as a dark pink color. The F_1 plant of WOB21 had white flowers (recessive). As expected the backcross with this crossed to 'Old Blush' supported a 0 dark pink:1 pink:1 white ratio (Table 4). The above results support the previous reports on flower color of pink being partially dominant.

Table 4. Chi square test for dark pink, pink, and white flower color.

Generation[z]	Dark Pink	Pink	White	Expected Ratio	χ^2
F_1	0	13	6	0:1:1	2.6 ^{NS}
BC13	25	51	13	1:2:1	5.1 ^{NS}
BC21	2	28	16	0:1:1	3.2 ^{NS}
BC26	18	65	23	1:2:1	5.9 ^{NS}

[z] Abbreviations for F_1 = 'Basye's Thornless' x 'Old Blush' and BC (13, 21, and 26) = 'Old Blush' x F_1 (13, 21, 26).
$^{NS,*, **, ***}$ Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Thus there is a major co-dominant gene conditioning the pink flower color in rose. Nevertheless the BC populations showed variation in color intensity and the color blends. This variation in flower color suggests that other factors, beyond this major gene, are involved in the final pink color of the rose flower. Quantitative analysis of flower color was not done in the BC populations because of the presence of the major gene pink to white flower color.

According to Griesbach (2002) and Wiering and De Vlaming (1984) floral pigmentation in petunia is quantitatively inherited with the single regulatory gene (An2) and three structural genes (Hf1, An6, and Fl). The genotype an2 an2 conditions white

flowers and the genotype An2 _ conditions pigment production. In ornamental peaches, three genes condition red, pink, and white flower color (Lammerts, 1945a). A similar genetic system seems to condition flower color in roses with a major gene conditioning pink color (Debener, 2003).

Flower Form

The presence of the double flower form has been reported to be conditioned by a dominant gene (recessive conditions single flower form) at one locus in rose (Crespel et al., 2002; Debener, 1999; Debener, 2003; Lammerts, 1945b; Swim, 1948). In this study, the parent 'Basye Thornless' had single and the other parent 'Old Blush' had double flower form. Segregation in the F_1 generation (1 double to 1 single) suggests that the 'Old Blush' parent is heterozygous for flower form. Eight of the F_1s had double and eleven had single flower form. The F_1 plants WOB13, WOB21, and WOB26 all have a single flower form (homozygous recessive) and the backcross generation (BC13, BC21, and BC26) segregated in a 1:1 for double:single flower form. Open pollinated 'Old Blush' (heterozygous) show the expected ratio of three double flowers per single flowering plant (Table 5).

Table 5. Chi square test for double and single flower form.

Generation[z]	Double	Single	Expected Ratio	χ^2
F_1	8	11	1:1	0.5 ^{NS}
BC13	39	47	1:1	0.7 ^{NS}
BC21	24	22	1:1	0.1 ^{NS}
BC26	54	44	1:1	1.0 ^{NS}
F_2 OB	7	3	3:1	0.1 ^{NS}

[z] Abbreviations for F_1 = 'Basye's Thornless' x 'Old Blush', BC (13, 21, and 26) = 'Old Blush' x F_1 (13, 21, 26), and F_2 OB = Open pollinated 'Old Blush'.
^{NS,*,**,***} Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

The above results support the previous reports on flower form (Crespel et al., 2002; Debener, 1999). The flower form seen above appears to be conditioned by one major gene. A large variation was seen in the number of petals found in the double flowers. Some of the double flowers even had more petals than both parents. Thus environmental interactions and additional genes influence the mean number of petals per flower (Debener, 1999; Debener, 2003; Garrod and Harris, 1974; Lammerts, 1945b; Morey, 1959; Rajapakse et al., 2001). In ornamental peaches, single flower form is completely dominant (D_1_) to double flower form, which is different than roses. The number of petals in the double flower form is conditioned by Dm_1 and Dm_2 alleles in ornamental peaches (Lammerts, 1945a). Quantitative analysis of number of petals was not done in the BC populations because of the presence of the major gene double to single flower form.

Presence of Stem Prickles

The presence of stem prickles has been reported to be conditioned by a dominant gene (recessive conditions no stem prickles) at one locus in rose (Debener, 1999; Debener, 2003; Rajapakse et al., 2001). In this study, the parent 'Basye Thornless' had no stem prickles and the other parent 'Old Blush' had stem prickles. Segregation in the F_1 generation (1 with prickles to 1 no stem prickles) suggests that the 'Old Blush' parent is heterozygous for stem prickles. Ten of the F_1s had stem prickles and nine had no stem prickles. The F_1 plants WOB13 and WOB26 have no stem prickles and the backcross generation (BC13 and BC26) support the expected 1:1 ratio for stem prickles:no prickles. The F_1 plant of WOB21 had stem prickles and the backcross generation (BC21) segregates in the ratio of 3:1 for stem prickles:no prickles. A backcross from the other direction was done by the hybridization of 'Basye's Thornless' with the F_1 plants of WOB13, WOB21, and WOB26. The backcross using 'Basye's Thornless' (BT) supports the above results since the plants from BT x WOB13 and BT x WOB26 have no stem prickles and about half the plants from BT x WOB21 have stem prickles (Table 6). The segregation of the open pollinated (selfed) 'Old Blush' (heterozygous) seedlings fit the expected ratio of three with stem prickles to one without stem prickles (Table 6).

Table 6. Chi square test for the presence of stem prickles.

Generation[z]	Present	Absent	Expected Ratio	χ^2
F_1	10	9	1:1	0.1 ^{NS}
BC13	73	64	1:1	0.6 ^{NS}
BC21	31	18	3:1	3.6 ^{NS}
BC26	80	90	1:1	0.6 ^{NS}
BT13	0	10	0:1	0 ^{NS}
BT21	46	55	1:1	0.8 ^{NS}
BT26	0	68	0:1	0 ^{NS}
F_2 OB	14	5	3:1	0 ^{NS}

[z] Abbreviations for F_1 = 'Basye's Thornless' x 'Old Blush', BC (13, 21, and 26) = 'Old Blush' x F_1 (13, 21, 26), BT (13, 21, 26) = 'Basye's Thornless' x F_1 (13, 21, 26), and F_2 OB = Open pollinated 'Old Blush'.

^{NS,*,**,***} Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

The above results support the previous reports on stem prickles (Crespel et al., 2002; Debener, 1999). Among the prickled types there is a wide variation in prickle density. Work by Crespel et al. (2002) suggests prickle density is conditioned by several QTL. A similar genetic system seems to condition prickle presence and density in blackberries (Pavlis and Moore, 1981). Quantitative analysis of prickle density was not done in the BC populations because of the presence of the major gene prickles to no stem prickles.

Summary

The reported modes of inheritance for flower color (pink co-dominant to white), flower form (double dominant to single), and stem prickles (prickles dominant to no prickles) agree with observed data. The segregation of the bloom (non-recurrent dominant to recurrent) habit trait showed a deficiency of recurrent blooming types. Potential explanations for this skewed segregation include the involvement of multiple genes, the interspecific nature of the population, and the possibility that the recurrent genotype either germinates poorly or dies more frequently at an early age as compared to non-recurrent genotypes.

Quantitative Analysis

Flower Size

The analysis of variance for flower diameter (mm) shows generation and genotype(generation) together explains 85% of the variation (Table 7). The mean of the F_1 plants (41.4 mm) was close to the midparent value (40.8 mm) indicating mainly additive inheritance (Table 8). A similar mode of inheritance was found for the flower size of the blueberry (Ritzinger and Lyrene, 1999).

Table 7. ANOVA for flower size for 'Basye's Thornless', 'Old Blush', F_1, BC13, BC21, and BC26.

Source	df	MS
Replication	3	69.6 ^{NS}
Generation	5	343.1 ***
Genotype(Generation)	125	75.1 *
Error	46	37.0
R-square		0.88

^{NS,*,**,***} Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Table 8. Mean flower size (mm) of 'Basye's Thornless' and 'Old Blush' and several derived generations.

Generation[z]	Mean	SE[y]	Range Low	Range High
OB	54.2	3.9	38	72
BC13	43.2	1.3	25	56
F_1	41.4	1.1	22	55
BC26	40.1	1.1	18	57
BC21	36.0	3.5	20	47
BT	27.3	3.5	19	33

[z] Abbreviations for OB = 'Old Blush', BT = 'Basye's Thornless', F_1 = BT x OB, and BC (13, 21, and 26) = OB x F_1 (13, 21, 26).
[y] SE = Standard error.

Petal Size

The analysis of variance for petal size (length mm) shows that generation and genotype(generation) together explains 76% of the variation (Table 9). The mean of the F_1 plants (20.8 mm) was only slightly lower than the midparent value (21.7 mm) indicating mainly additive inheritance (Table 10).

The good correlation (r = 0.79) between rose petal length and flower size suggests these traits are conditioned by linked genes or by the same genes since the length of the petal in part determines the diameter of the flower. According to Ritzinger and Lyrene (1999) the size of blueberry flowers is also inherited in an additive mode.

Table 9. ANOVA for petal size for 'Basye's Thornless', 'Old Blush', F_1, BC13, BC21, and BC26.

Source	df	MS
Replication	3	44.3 ^{NS}
Generation	5	58.1 *
Genotype(Generation)	136	24.4 ^{NS}
Error	54	18.2
R-square		0.81

^{NS,*,**,***} Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Table 10. Mean petal size (mm) of 'Basye's Thornless' and 'Old Blush' and several derived generations.

			Range	
Generation[z]	Mean	SE[y]	Low	High
OB	27.8	2.0	18	38
BC13	21.8	0.7	13	33
F_1	20.8	0.6	9	35
BC26	20.8	0.6	11	35
BC21	16.3	2.0	12	20
BT	15.6	2.0	12	24

[z] Abbreviations for OB = 'Old Blush', BT = 'Basye's Thornless', F_1 = BT x OB, and BC (13, 21, and 26) = OB x F_1 (13, 21, 26).
[y] SE = Standard error.

Flowers per Stem

The analysis of variance for flowers per stem shows that generation and genotype(generation) together explains 81% of the variation. However, the replication effect accounted for 4% of the variation (Table 11). The mean of the F_1 plants (2 flowers per stem) was the same as the midparent value (2 flowers per stem) and both parents (2 flowers per stem) inheritance could not be determine (Table 12).

Previous studies could not be found about the genetics of flowers per stem. The replication was significant for flowers per stem. Replication three and four had fewer flowers per stem than replication one and two (Table 13). Replications three and four had less favorable environmental conditions (shading by trees and poor drainage) than replications one and two that could have caused fewer flowers to develop. To make better sense of the inheritance of flowers per stem the replication differences within the environment should be limited by letting the plants get the same amount of sunlight and having more uniform drainage.

Table 11. ANOVA for flowers per stem for 'Basye's Thornless', 'Old Blush', F_1, BC13, BC21, and BC26.

Source	df	MS
Replication	3	1.8 *
Generation	5	1.7 NS
Genotype(Generation)	112	0.8 *
Error	40	0.5
R-square		0.86

NS,*, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Table 12. Mean flowers per stem of 'Basye's Thornless' and 'Old Blush' and several derived generations.

			Range	
Generation[z]	Mean	SE[y]	Low	High
F_1	2	0.1	1	4
BT	2	0.4	1	3
OB	2	0.3	1	3
BC26	2	0.1	1	3
BC13	2	0.1	1	4
BC21	2	0.5	1	3

[z] Abbreviations for OB = 'Old Blush', BT = 'Basye's Thornless', F_1 = BT x OB, and BC (13, 21, and 26) = OB x F_1 (13, 21, 26).
[y] SE = Standard error.

Table 13. Mean flowers per stem in College Station replications.

			Range	
Replication	Mean	SE[z]	Low	High
1	2.2	0.1	1	4
2	2.1	0.1	1	3
3	1.8	0.1	1	3
4	1.7	0.1	1	3

[z] SE = Standard error.

Leaflet Number

The analysis of variance for leaflet number shows that generation and genotype(generation) together explains 76% of the variation. Environment x genetic [environment x generation and environment x genotype(generation)] were not significant, which indicates leaflet number is stable across environments (Table 14). The mean of the F_1 plants (8 leaflets) was higher than the midparent value (7.5 leaflets) indicating partial dominance (0.5) towards a greater number of leaflets per leaf by the parent 'Basye's Thornless' (Table 15).

Table 14. ANOVA for leaflet numbers for 'Basye's Thornless', 'Old Blush', F_1, BC13, BC21, and BC26.

Source	df	MS
Environment	1	0.2 ^{NS}
Replication(Environment)	6	1.0 ^{NS}
Generation	5	44.7 ***
Genotype(Generation)	134	1.7 ***
Environment x Generation	5	0.7 ^{NS}
Environment x Genotype(Generation)	100	0.5 ^{NS}
Error	124	0.7
R-square		0.85

^{NS,*,**,***} Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Table 15. Mean leaflet number of 'Basye's Thornless' and 'Old Blush' and several derived generations.

			Range	
Generation[z]	Mean	SE[y]	Low	High
BT	9	0.3	7	11
F_1	8	0.1	7	11
BC21	7	0.2	5	9
BC26	7	0.2	5	9
BC13	7	0.2	5	9
OB	6	0.4	5	7

[z] Abbreviations for OB = 'Old Blush', BT = 'Basye's Thornless', F_1 = BT x OB, and BC (13, 21, and 26) = OB x F_1 (13, 21, 26).
[y] SE = Standard error.

The only previous study found on the inheritance of leaflet number was found for soybean. In this case, the seven leaflet condition (lf_2) and five leaflet state (lf_1) are conditioned by two single major genes. The three leaflet state is conditioned by at least one dominant allele (Lf_2 and Lf_1) which has complete to partial dominance over the 5 and 7 leaflet states. Fehr (1972) showed that a three leaflet by a seven leaflet soybean cross gave a 3:1 ratio with three leaflets being dominant. However, in this rose study the leaflet number is partially dominant toward the greater leaflet number. When the data was recorded to correspond to the nearest odd leaflet number, the rose leaflet number data did not fit into a recognizable qualitative pattern (Table 16). Thus rose leaflet number appears to be inherited in a quantitative fashion.

Table 16. Number of plants with leaflet numbers of five, seven, and nine for F_1, BC13, BC21, BC26, and 'Old Blush' OP.

	Parents	Number of Leaflets		
Generation[z]	Leaflet	Five	Seven	Nine
F_1	9 x 5	0	10	9
BC13	5 x 7	7	30	2
BC21	5 x 9	4	31	3
BC26	5 x 9	10	23	7
F_2 OB	5 x 5	12	7	0

[z] Abbreviations for F_1 = 'Basye's Thornless' x 'Old Blush', BC (13, 21, and 26) = 'Old Blush' x F_1 (13, 21, 26), and F_2 OB = 'Old Blush' open pollinated.

Powdery Mildew

The analysis of variance for powdery mildew (*Podosphaera pannosa*) resistance for May of 2004 shows that generation and genotype(generation) together explains 54% of the variation whereas the variation due to environmental effects environment and replication(environment) together explains 3% of the variation (Table 17). The mean of the F_1 plants (0.6) was similar to the midparent value (0.5) indicating additive inheritance (Table 18). This environment effect combined with the low values for powdery mildew incidence would indicate that the inoculum was low and not evenly dispersed over the environments and the replications within the environments.

Table 17. ANOVA for powdery mildew resistance for 'Basye's Thornless', 'Old Blush', F1, BC13, BC21, and BC26.

Source	df	MS
Environment	1	2.9 **
Replication(Environment)	6	0.9 *
Generation	5	1.5 **
Genotype(Generation)	133	0.9 ***
Environment x Generation	5	0.4 NS
Environment x Genotype(Generation)	108	0.5 NS
Error	124	0.4
R-square		0.81

NS,*, **, *** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Table 18. Mean powdery mildew resistance[z] of 'Basye's Thornless' and 'Old Blush' and several derived generations.

			Range	
Generation[y]	Mean	SE[x]	Low	High
F_1	0.6	0.1	0	4
OB	0.5	0.3	0	2
BC21	0.5	0.1	0	3
BT	0.5	0.2	0	2
BC13	0.3	0.1	0	3
BC26	0.2	0.1	0	1

[z] Disease rating 0 = no disease, 1 = one or two isolated infections, 2 = slight infection throughout plant, 3-7 = percent of leaves infected, 8 = most foliage, stems, and peduncles with infection, and 9 = heavy infection throughout plant.
[y]Abbreviations for OB = 'Old Blush', BT = 'Basye's Thornless', F_1 = BT x OB, and BC (13, 21, and 26) = OB x F_1 (13, 21, 26).
[x] SE = Standard error.

The Overton site had higher levels of powdery mildew as compared to the College Station site (Table 19). This was probably is due to the fact that in May 2004, Overton had cooler average day (day 27.9 ^{o}C) and night (18.6 ^{o}C) temperatures that were closer to the optimal disease development conditions (days 26.7 ^{o}C and night 15.5 ^{o}C) than did College Station (Appendix A and B).

Table 19. Mean powdery mildew resistance[z] in Overton and College Station, TX environments.

			Range	
Environment	Mean	SE[y]	Low	High
Overton	0.5	0.04	0	4
College Station	0.3	0.04	0	3

[z] Disease rating 0 = no disease, 1 = one or two isolated infections, 2 = slight infection throughout plant, 3-7 = percent of leaves infected, 8 = most foliage, stems, and peduncles with infection, and 9 = heavy infection throughout plant.
[y] SE = Standard error.

Podosphaera pannosa has at least eight physiological races. Resistance to race 9 has been reported to be conditioned by a dominant gene Rpp1 although additional genetic factors were also hypothesized to control partial resistance (Debener, 2003; Linde and Debener, 2003). The number or identity of *Podosphaera pannosa* races present in the College Station and Overton environments are not known. Thus the difference in the level of disease incidence could be determined by both major and minor genes in these progeny. However, since both of the parents ('Basye's Thornless' and 'Old Blush') are susceptible it is likely that no major dominant genes for resistance exist in these populations. Nevertheless, in 2004 because the incidence was low, the inheritance of powdery mildew is difficult to determine from this data. Inoculating

leaves from each plant with *Podosphaera pannosa* would give a better idea of which plants are resistant. Leaf inoculation would eliminate this problem of uneven distribution of the inoculum that was seen in this field experiment.

Black Spot

The black spot (*Diplocarpon rosae*) ratings in the year 2004 were examined separately for the early (May), mid (July), and late (October) season black spot incidence. May had the smallest and October had the largest amount of black spot lesion development (Table 20). The rating scale evaluates both the number (amount) of lesions and the lesion size to give an assessment of black spot infection intensity.

In the months of May and July the black spot disease pressure was low (Table 20). This resulted in an uneven distribution of disease pressure between sites as well as within each site as indicated by the significance of the environment and/or replication(environment) effects for May and July. Only for the October ratings these effects are not significant indicating a more uniform distribution of disease pressure (Table 21). In addition, the ratings for October show a better separation (range) of susceptible and resistant plants, consequently this month was used in the analysis of black spot resistance (Table 20).

Table 20. Mean black spot resistance[z] of 'Basye's Thornless' and 'Old Blush' and several derived generations.

	May				July				October			
			Range				Range				Range	
Generation[y]	Mean	SE[x]	Low	High	Mean	SE[x]	Low	High	Mean	SE[x]	Low	High
OB	2.3	0.3	0	5	2.5	0.3	0	4	4.4	0.4	2	7
BC26	1.9	0.2	0	5	2.1	0.1	0	5	3.3	0.2	1	6
BC21	2.0	0.2	0	6	2.1	0.1	0	5	2.6	0.2	1	6
BC13	1.6	0.1	0	6	1.8	0.1	0	4	2.6	0.2	1	7
F_1	0.8	0.1	0	4	1.2	0.1	0	4	2.8	0.1	0	6
BT	0.0	0.3	0	0	0.7	0.3	0	2	1.0	0.3	0	2
Overall mean	1.4				1.7				2.8			

[z] Disease rating 0 = no disease, 1 = one or two isolated infections, 2 = slight infection throughout plant, 3-6 = percent of leaves infected, 7 = most foliage infected except most distal, 8 = all foliage infected, and 9 = all foliage infected, heavy defoliation, plant vigor reduced.

[y] Abbreviations for OB = 'Old Blush', BT = 'Basye's Thornless', F_1 = BT x OB, and BC (13, 21, and 26) = OB x F_1 (13, 21, 26).

[x] SE = Standard error.

Table 21. ANOVA for black spot resistance for 'Basye's Thornless', 'Old Blush', F1, BC13, BC21, and BC26.

	May		July		October	
Source	df	MS	df	MS	df	MS
Environment	1	63.6 ***	1	2.6 *	1	0.2 NS
Replication(Environment)	6	0.6 NS	6	3.0 ***	6	1.0 NS
Generation	5	24.1 ***	5	12.1 ***	5	16.8 ***
Genotype(Generation)	134	1.6 *	132	1.2 NS	132	1.7 NS
Environment x Generation	5	5.2 ***	5	3.0 **	5	3.3 *
Environment x Genotype(Generation)	112	1.1 ***	105	1.0 **	102	1.4 **
Error	126	0.4	119	0.6	123	0.9
R-square		0.92		0.85		0.82

NS,*,**,*** Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

In recent studies according to Debener (1998), *Diplocarpon rosae* has at least five physiological races. Two single dominant genes Rdr1 and Rdr2 have been identified to condition resistance (Debener, 2003). The number of *Diplocarpon rosae* races or which races present in the College Station and Overton environments are not known. 'Basye's Thornless' appears to have stable resistance over environments and years by having low ratings of black spot. A possible confounding factor is the fungus disease cercospora (*Cercospora puderi* B.H. Davis) which looks similar to black spot. This disease has a circular leaf spot with lighter color center as compared to black spot (Horst, 1983). Cercospora was observed mostly on 'Basye's Thornless', but also on F_1s and backcross progenies. Black spot could have been mistaken for cercospora, giving 'Basye's Thornless' a higher rating.

The analysis of variance for black spot resistance for Oct. 2004 shows that generation and genotype(generation) together explains 73.3% of the variation. The environment x genetic interactions [environment x generation and environment x genotype(generation)] explains 18.5% of the variation (Table 21). The mean of the F_1 plants (2.8) were similar to the midparent value (2.7) indicating mainly additive inheritance (Table 20).

The environment x generation interaction seen in October could be due to the 'Basye's Thornless', 'Old Blush', and BC13 having a higher mean in Overton compared to College Station and the F_1s, BC21, and BC26 having a higher mean in College Station compared to Overton (Table 22 and Fig 1). Although the rankings of the genotypes with intermediate resistance may change some, since the genetic effect explains almost two

times the variation as compared to the interaction effect, the initial selection could effectively be done at one environment to eliminate the most susceptible plants. The resistance of these selections would need to be confirmed with trials at other sites.

Table 22. October mean black spot resistance[z] for environment x genetic interaction of 'Basye's Thornless' and 'Old Blush' and several derived generations in College Station and Overton, TX

	College Station				Overton			
			Range				Range	
Generation[y]	Mean	SE[x]	Low	High	Mean	SE[x]	Low	High
OB	4.3	0.3	2	7	4.5	0.3	3	6
BC26	3.5	0.1	1	6	3.1	0.1	1	5
F1	3.1	0.1	1	6	2.5	0.1	0	6
BC21	2.8	0.1	1	5	2.5	0.1	1	6
BC13	2.3	0.1	1	4	2.8	0.1	1	7
BT	0.9	0.2	0	1	1.1	0.2	0	2

[z] Disease rating 0 = no disease, 1 = one or two isolated infections, 2 = slight infection throughout plant, 3-6 = percent of leaves infected, 7 = most foliage infected except most distal, 8 = all foliage infected, and 9 = all foliage infected, heavy defoliation, plant vigor reduced.

[y] Abbreviations for OB = 'Old Blush', BT = 'Basye's Thornless', F_1 = BT x OB, and BC (13, 21, and 26) = OB x F_1 (13, 21, 26).

[x] SE = Standard error.

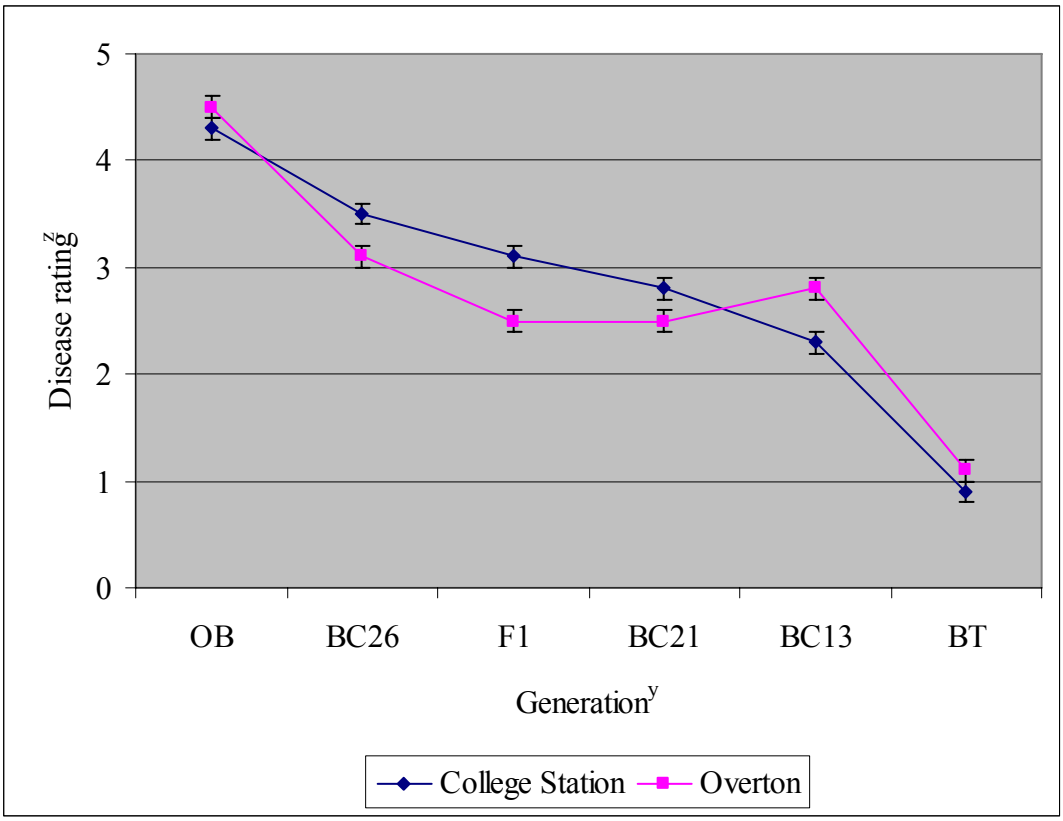

Fig. 1. Mean black spot rating for 'Basye's Thornless' and 'Old Blush' and several derived generations in College Station and Overton, TX during October 2004.

[z] Disease rating 0 = no disease, 1 = one or two isolated infections, 2 = slight infection throughout plant, 3-6 = percent of leaves infected, 7 = most foliage infected except most distal, 8 = all foliage infected, and 9 = all foliage infected, heavy defoliation, plant vigor reduced.
[y] Abbreviations for OB = 'Old Blush', BT = 'Basye's Thornless', F_1 = BT x OB, and BC (13, 21, and 26) = OB x F_1 (13, 21, 26).

Malek and Debener (1998) did a qualitative study of black spot resistance by inoculating rose leaves with *Diplocarpon rosae* and scoring for growth of the mycelium. The roses where scored as resistant or susceptible and compared as ratios. In the present data, if incidence were grouped as rating of two, the highest rating for BT, or less as resistant and more than two being susceptible, the F_1s in College Station fit a 1:1 and 3:1

ratio for resistant:susceptible and F_1s in Overton fit a 1:1 ratio for resistant:susceptible. All of the backcross generations except BC26 in College Station also fit 1:1 ratio for resistant:susceptible and the BC26 in College Station fit a 3:1 ratio (Table 23 and 24). The ratios seen for the F_1s and backcrosses would indicate that 'Basye's Thornless' has a major gene for resistance to black spot and is heterozygous for this gene.

Black spot was analyzed as a quantitative trait with the assumption that the environment influences incidence or that many genes are involved (horizontal resistance). However, the environmental variance was low for black spot and the resistant to susceptible ratios fit a qualitative analysis.

Table 23. Chi square test for black spot resistance in College Station, TX.

Generation[z]	Resistant	Susceptible	Expected Ratio	χ^2
F_1	12	7	1:1	1.3 ^{NS}
BC13	11	22	1:1	3.7 ^{NS}
BC21	16	14	1:1	0.1 ^{NS}
BC26[y]	25	7	1:1	10.1 **

[z] Abbreviations for F_1 = 'Basye's Thornless' x 'Old Blush' and BC (13, 21, and 26) = 'Old Blush' x F_1 (13, 21, 26).
[y] BC26 fits a 3:1 ratio with $\chi^2 = 0.2$.
$^{NS,*, **, ***}$ Nonsignificant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively.

Table 24. Chi square test for black spot resistance in Overton, TX.

Generation[z]	Resistant	Susceptible	Expected Ratio	χ^2
F_1	8	11	1:1	0.5 ^{NS}
BC13	19	14	1:1	0.8 ^{NS}
BC21	20	15	1:1	0.7 ^{NS}
BC26	21	15	1:1	1.0 ^{NS}

[z] Abbreviations for F_1 = 'Basye's Thornless' x 'Old Blush' and BC (13, 21, and 26) = 'Old Blush' x F_1 (13, 21, 26).

Summary

Generation and/or genotype(generation) explained most of the variation for flower size, petal size, flowers per stem, leaflet number, powdery mildew resistance, and black spot resistance. The environmental effects [environment, replication(environment), and/or replication] were significant for flowers per stem, and powdery mildew resistance. The environment x generation and environment x genotype(generation) were significant for black spot resistance.

The traits flower size, petal size, flower per stem, leaflet number, powdery mildew, and black spot resistance have high genetic variation and low environment variation and could be selected for in one environment. For the number of flowers per stem, the generation is not significant due to both parents (OB and BT) having no variation of two flowers per stem. The flowers per stem had significant replication due to different environmental conditions within environment. Powdery mildew resistance in this experiment had low inoculum and/or poor distribution of inoculum at the locations used making environmental variation [environment and replication(environment)] significant. An increase in the natural powdery mildew inoculum in the field or inoculating leaves in the laboratory would be needed to assess the inheritance of powdery mildew. Black spot resistance had different generation and/or genotype rankings between the two environments making environment x genetic interaction significant. Black spot resistance was also shown to fit a qualitative analysis with resistant to susceptible ratios.

Additive gene action (no dominance) was observed for flower size, petal size, black spot resistance, and powdery mildew resistance. The gene action of partial dominance was observed for leaflet number. Gene action for flowers per stem could not be determined due to lack of variation.

CHAPTER V

CONCLUSION

In 2004, morphological flower, stem and leaf, and disease resistance traits were observed. The qualitative traits of bloom habit, flower color, flower form, and stem prickles were observed in College Station, TX. Flower color, flower form, and stem prickles fit the reported single gene inheritance pattern whereas the bloom habit did not fit the reported single gene inheritance. Reasons bloom habit did not fit the expected ratios could be the involvement of multiple genes, the interspecific nature of the population, and/or that the recurrent plants having poor germination or being weaker plants that die more often at an early age.

The quantitative traits of flower size, petal size, and flowers per stem were measured in College Station, TX. Flower size and petal size had a high genetic effect, suggesting that these traits are stable within environment. Flowers per stem had significant replication effect due to different environmental conditions which made trait not stable within environment. The F_1s had mean values near the midparent value indicating additive inheritance for flower size and petal size. Inheritance could not be determined for flowers per stem since lack of variation for the number of flowers per stem (Table 25).

Table 25. Quantitative analysis for flower size, petal size, and flowers per stem in College Station, TX.

Trait	Replication	Generation/ genotype	Mode of action
Flower size	NS	85%	Additive
Petal size	NS	76%	Additive
Flowers per stem	4%	81%	-

The quantitative traits of leaflet number, powdery mildew resistance, and black spot resistance were measured in College Station and Overton, TX. Leaflet number had a high genetic effect suggesting that this trait is stable across environments. Powdery mildew resistance had significant environmental effects likely caused by low or poor dispersal of inoculum. The means for powdery mildew incidence were significantly different between the two environments, but the ranking of the generations stayed the same allowing selection at one site. Black spot resistance had an environment x genetic interaction. The means for black spot resistance may or may not be the same between the two environments, but the ranking of the generations were different in each environment. However, the genetic effect is about two times the environment x genetic interaction which would allow selection at one site. The selected black spot resistant progenies would need to be tested in additional sites to verify resistance. Black spot was also shown to fit a qualitative analysis with resistant to susceptible ratios.

The F_1s had mean values near the midparent value indicating additive inheritance for black spot resistance and powdery mildew resistance. The F_1s had mean value greater than the midparent value indicating partial dominance for leaflet number (Table 26).

Table 26. Quantitative analysis for leaflet number, powdery mildew resistance, and black spot resistance in College Station and Overton, TX.

Trait	Environment/ replication	Generation/ genotype	Environment x generation/ genotype	Mode of action
Leaflet number	NS	76%	NS	Partial dominance
Powdery mildew resistance	3%	54%	NS	Addititve
Black spot resistance	NS	53%	27%	Addititve

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APPENDIX A

Appendix A. Temperature and rainfall history for College Station, TX 2004.

2004 CS-GH	High temp ^{o}C	Low temp ^{o}C	Ave temp ^{o}C	Rain (cm)	Days rained
January	16.9	6.9	11.9	11.5	10
February	15.0	5.6	10.3	15.0	14
March	24.2	13.8	19.0	7.1	11
April	25.8	15.1	20.4	10.7	9
May	29.6	19.6	24.6	19.9	9
June	30.9	22.6	26.8	29.8	18
July	33.5	23.1	28.3	5.9	5
August	33.4	22.4	27.9	6.5	8
September	32.9	21.2	27.1	0.7	6
October	29.8	20.2	25.0	9.7	12
November	20.7	10.8	15.8	23.4	11
December	17.4	5.3	11.4	2.7	6
Total				142.9	119

According to Office of the Texas State Climatologist, Department of Atmospheric Science, Texas A&M University (3 Mar. 2005).

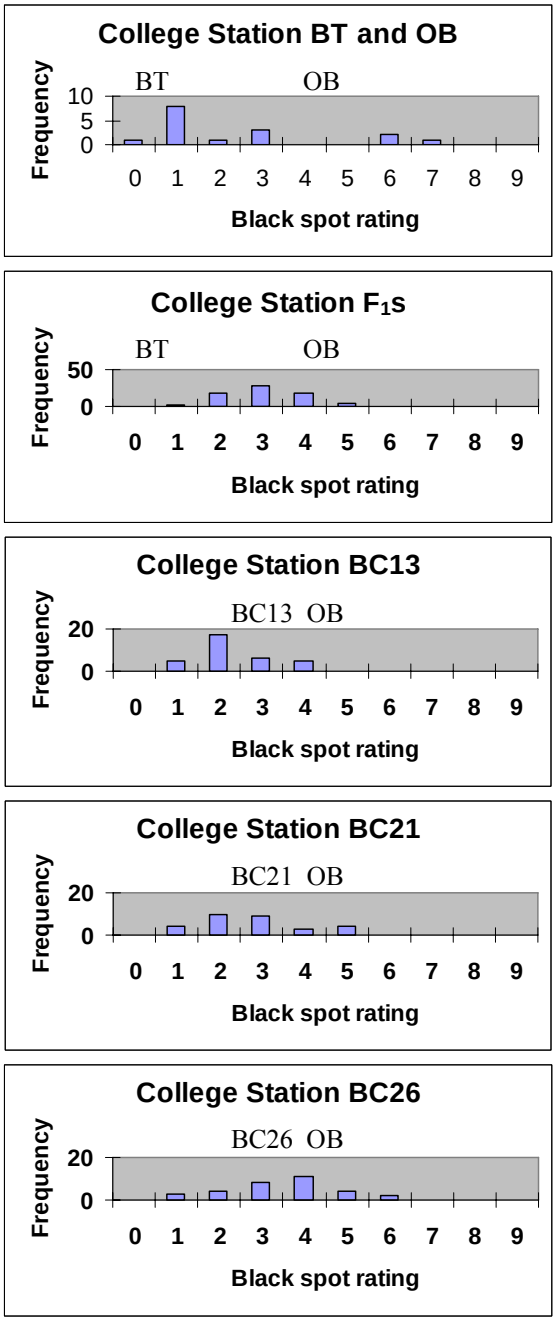
APPENDIX B

Appendix B. Temperature and rainfall history for Overton, TX 2004.

2004 OV	High temp ^{o}C	Low temp ^{o}C	Ave temp ^{o}C	Rain (cm)	Days rained
January	14.9	4.3	9.3	8.6	9
February	12.8	3.2	7.8	14.8	15
March	22.7	11.3	16.9	10.3	14
April	24.0	13.0	18.2	14.6	9
May	27.9	18.6	22.9	12.0	6
June	29.9	21.2	25.0	16.5	15
July	32.4	21.9	26.9	3.4	6
August	31.4	20.0	25.4	6.7	8
September	30.9	17.9	24.0	3.1	3
October	27.2	18.4	22.2	11.3	10
November	18.9	9.6	14.0	19.9	12
December	15.6	3.2	9.0	5.5	6
Total				126.8	113

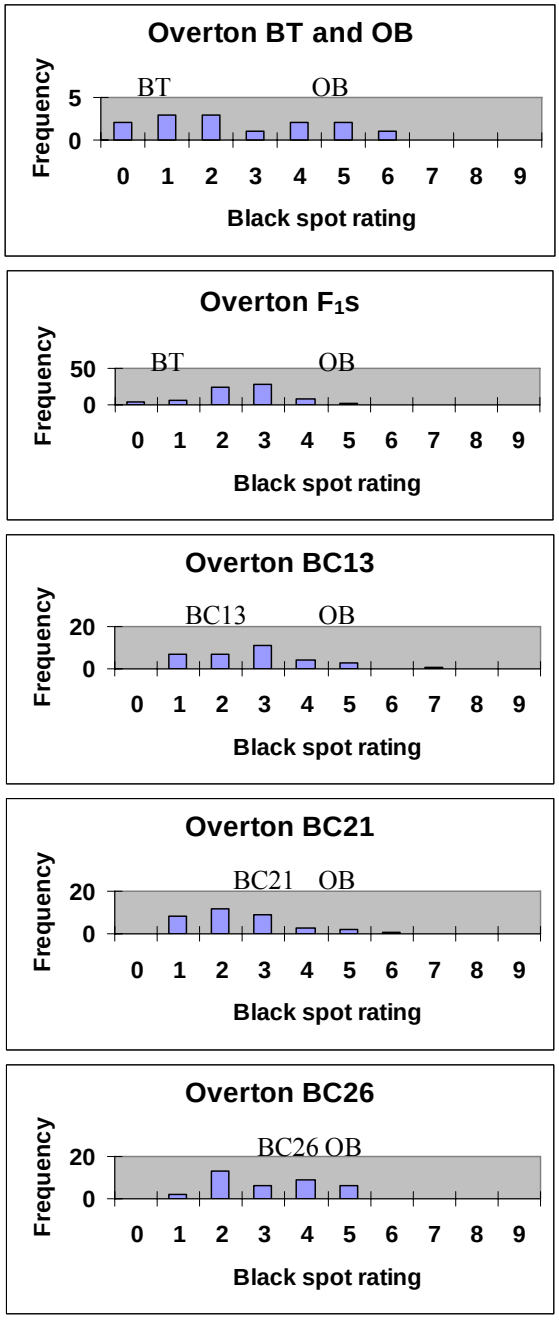
According to Texas A&M University Agricultural Research and Extension Center Overton, TX (30 Mar. 2005).

APPENDIX C



Appendix C. Black spot ratings for 'Basye's Thornless', 'Old Blush', and several derived generations in College Station, TX during October 2004.

APPENDIX D



Appendix D. Black spot ratings for 'Basye's Thornless', 'Old Blush', and several derived generations in Overton, TX during October 2004.

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