HERITABILITY OF PLANT ARCHITECTURE IN DIPLOID ROSES (*ROSA* SPP.)

A Thesis

by

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MASTER OF SCIENCE

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ABSTRACT

Plant architecture is very important because it helps understand the plant organization and the interaction between the plant and the environment. In the preliminary study with four F_1 families, 13 architectural traits were evaluated, and six traits were calculated in May of 2014 in College Station, TX to estimate variability, phenotypic correlations and principle components. All architectural traits except the length of secondary vegetative part, the length of secondary shoots, the branching angle between primary and secondary shoots and the internode length of both order level shoots differed among the four rose populations. The same traits on different order level shoots were generally correlated as were some of the different traits. The most common inflorescence structure type observed among rose seedlings was a cyme, although other types such as a reversed raceme, raceme, solitary flower and even mixed types and unknown types were observed. Based on the result of PCA, the attribute that best explain the variability observed in our rose seedlings are the number of nodes on the secondary shoot, the length of the reproductive part and the internode length on primary and secondary shoots. By combining the preliminary data with that from previous studies, we chose six architectural traits for subsequent study. They are plant height, the number of primary shoots, the length of the primary shoots, the number of nodes on the primary shoots, the number of secondary shoots per primary shoot, and the number of tertiary shoots per primary shoot.

In 2015, six rose plant architectural traits were evaluated in May and December in College Station, TX to estimate variability and heritability. Most traits showed a substantial amount of variability. A random effects model Restricted Maximum Likelihood (REML) analysis was used to estimate the genetic components, narrow sense heritability and broad sense heritability. Architectural traits demonstrated low to moderate narrow sense heritability (0.12-0.50) and low to high broad sense heritability (0.25-0.92). Traits with low narrow sense heritability but moderately high to high broad sense heritability (number of primary shoots, the length of primary shoots and the number of nodes on the primary shoot) indicate an important non-additive genetic component. The number of nodes on the primary shoots, and the number of secondary and tertiary shoots per primary shoot were greatly affected by the genotype by environment interaction. Most families, except for the three with 'Vineyard Song' as a parent, did not increase in the number of nodes on the primary shoot over the season. In contrast, 11 out of 13 families had more secondary and tertiary shoots form during the year. Even among those with increased numbers of secondary and tertiary shoots, the number varied among families. For these traits selection would need to be done in both seasons whereas with plant height, shoot length and the number of primary shoots selection in either the early or late season would be effective. A comparison of desirable and undesirable plant growth types indicated that the key differences were in the number of primary shoots and in the density of secondary/tertiary shoots on the primary shoot, with more desirable types having more than thirty primary shoots with multiple secondary/tertiary shoots.

DEDICATION

This thesis is dedicated to four most special people in my life without whom, I could not be who I am today:

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Grandmother: Xiufang Lei

Father: Jianwei Wu

Mother: Yun Hu

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CHAPTER I

INTRODUCTION AND LITERATURE REVIEW

1.1 Rose is an important ornamental crop

Roses are members of the Rosaceae, the most important horticultural family in the world, admired for their great diversity and various floral characteristics throughout history. They are the world's most important ornamental crops with a production value of about 24 billion Euros (Heinrichs, 2008). In the $2.81 billion wholesale US shrub market, garden and landscape roses together contribute approximate $400 million in bare root and container production (AmericanHort, 2014).

There are four subgenera under the genus *Rosa*, which has about 100-250 species and over 30,000 commercial cultivars with a wide interspecific and intraspecific cross compatibility (Blechert and Debener, 2005; Clains, 2000). The ploidy level in *Rosa* ranges from diploid to decaploid (Byrne and Crane, 2003; Spiller et al., 2011; Jian et al., 2010; Zlesak, 2009; Ueckert et al., 2015). Most commercial cultivars are diploid, triploid, and tetraploid hybrids, which were obtained from multiple wild diploid and a few tetraploid rose species (Zhang et al., 2006). The genus is distributed throughout the temperate regions of the Northern Hemisphere (Krussmann, 1981). Cultivated roses (*Rosa* L.) are the world's most popular garden and cut flower plants. Garden roses exist in many forms including hybrid teas, shrubs, and polyanthas, which display vast diversity of colors and forms and thus serve a multitude of landscape uses. Breeding and genetic work of roses is active with much effort expended at developing sustainable roses with high aesthetic value and good adaptability for garden use (Byrne, 2014).

The role roses play in landscapes is extensive with their use adorning road sides, public parks and residential areas. Garden roses provide aesthetic value throughout the growing season. Both vegetative and reproductive organs are important in the development of an ornamental plant which is of great visual quality. In spite of the economic importance of roses relative to other ornamentals, they are of minor importance when compared to major food crops and consequently less well studied (De Vries, 1996).

1.2 Plant architecture and its importance

The architecture of a plant depends on the relative arrangement of plant organs and its growing environment. It is the expression of a balance between developing processes within an organism and external influences exerted by the environment. By analyzing plant architecture, we will be able to identify the modes of both internal processes and external influences, and make full use of them to realize the breeding goal (Barthélémy and Caraglio, 2007). Plant architectural characteristics have been shown to be linked to crop yield, and for roses, plant architecture affects their ornamental value and flower productivity. Therefore, plant architectural analysis appears to be particularly well adapted to assessing both economic and aesthetic value of an ornamental crop such as rose, which has a complex architecture (Crespel et al., 2014).

The scientific research on plant architecture started about 30 years ago (Oldeman, 1974; Halle et al., 1978). Early studies were focused on the above-ground vegetative structures of tropical trees (Halle and Oldeman, 1970). Since then, the

concept of plant architecture has been widely acknowledged and utilized for studying plant form, structure and their traits. However, data acquisition of plant architecture is both time-consuming and labor-intensive (Godin, 2000). In the past two decades, the development of high-performance computers has made it possible to analyze plant growth by simulation techniques, which provide advanced means of denoting and presenting plant architecture (tree graphs, multi-scale graphs, object-oriented representations, matrices, sets of digitized points) (Godin, 2000). Applicable to any kind of plant, architectural analysis has proved to be one of the most efficient means currently available for the study of the organization of complex arborescent plants (Barthélémy and Caraglio, 2007).

1.3 Work on plant architecture of roses

For ornamental crops like roses, plant architecture is the key factor determining the appearance of the plant and its commercial value (Demotes-Mainard et al., 2009). Previous research has shown that the plant architecture of the rose can be altered by modification of light intensity. (Kawamura and Takeda, 2002; Niinemets and Lukjanova, 2003), nitrogen deficiency (Huché-Thélier et al., 2011), temporary water restriction (Demotes-Mainard et al., 2013), mechanical stimulation (Morel et al., 2012) and by temperature regimes (summer-like versus winter-like conditions) (Khayat and Zieslin, 1982).

Roses have been characterized by both quantitative and qualitative morphological traits such as size, shape, and the color of petals, hips and sepals,

inflorescence architecture, the length of the pedicel, glandular hairs, and prickles (Crespel et al., 2013; Girault et al., 2008). In recent years, researchers have constructed models of plant architecture in rose bushes to describe their development which has been helping us understand the plasticity of rose plant architecture. Demotes-Mainard et al., (2009) set up a model to describe the mode of action of organ development and coordination in the primary shoot of roses. The traits they measured were internodes and leaflets. The result of their research could be fitted to a linear-plateau model. This research not only contributes to analyzing the response of phenotypic development of roses to the genotype (G), environment (E) and genotype × environment (G × E) interactions, but also has led to the simulation of organs by constructing a virtual plant model based on a radiative transfer model (Chelle and Andrieu, n.d.).

The plant architecture was objectively characterized by breaking down the plant into traits of the growth and branching processes. These traits themselves could be morphologically characterized by their number, length and diameter, by the way they are connected, and by their positioning in space (i.e., shoot angles). Based on this, roses with different shapes (from upright to prostrate) were analyzed for plant architecture (Crespel et al., 2013). The architecture of the inflorescence is a crucial characteristic because it is largely linked to plant productivity (Upadyayula et al., 2006a, b; Brown et al., 2006). However, the genetic determinism of inflorescence architecture is rarely studied, especially in woody perennial plants. A recent QTL analysis (Kawamura et al., 2011) of the pattern of rose inflorescence development revealed substantial genetic variations in

inflorescence traits of garden roses with high broad-sense heritabilities (0.82-0.93) and significant genotypic correlations for most traits.

Crespel et al., (2014) published the result of their preliminary study on the effects of genotype and year factors, and their interaction, on six architectural variables. Highly significant genotype (G), year (Y) and G × Y interaction were detected for all variables. Broad-sense heritability estimates were moderate to high (48% to 98%). This study resulted in a hypothesis that genetic analysis based on segregating progeny may be useful to explain architectural variability of rose plants. One study with a tetraploid cut flower germplasm showed that for some traits such as number of petals, the G × E interaction is low and the heritability is high. While for others such as stem width, the interaction is higher so that selection for or against these traits is suggested to be done at the production location (Gitonga et al., 2014)

CHAPTER II

PRELIMINARY STUDY ON PLANT ARCHITECTURAL TRAITS IN DIPLOID ROSES

2.1 Synopsis

Thirteen architectural traits were evaluated in May of 2014 in College Station, TX on seedlings from four F_1 families to estimate variability and phenotypic correlations. Six architectural traits were calculated based on the 13 traits, and then all 19 traits were subjected to statistical analysis. The vegetative traits evaluated on both primary and secondary shoots were the length of the vegetative part, the number of nodes on the vegetative part and the internode length of the shoot. The reproductive traits evaluated on both primary and secondary shoots were the length of the reproductive part, the number of inflorescence nodes, and the number of flowers on the terminal inflorescence. The traits evaluated on the shoot of both order level shoots included the length of the shoot and the number of nodes on the shoot. The branching angles which included the angle between the primary and the secondary shoots, and that between the secondary and the tertiary shoots were evaluated. Inflorescence structure type was characterized at the plant level.

Most architectural traits except the length of secondary vegetative part, the length of secondary shoot, branching angle between primary and secondary shoots, and the internode length of both order level shoots differed among the four rose populations. The same traits on different order level shoots were generally correlated. Significant

correlations were also found between the length of the part/shoot (vegetative, reproductive and shoot) and the number of nodes on the part/shoot (vegetative, reproductive and shoot).

Based on the principal component analysis, the important variables that explained the variability of plant architecture in the preliminary study included: the length of the primary and secondary reproductive parts, the internode length of the secondary shoot, and the number of nodes on the secondary shoot.

The most common inflorescence structure type observed among rose seedlings was a cyme, others such as a raceme, reversed raceme, solitary flower, mixed types (cyme + reversed raceme, cyme + solitary, reversed raceme + solitary) and even a couple of unknown inflorescence types were also observed.

A selection of architecture traits that are most relevant for characterizing rose plant architecture were made based on our statistical analysis combined with previous studies. The most important traits include the length of shoots, the number of nodes on the shoot, branching angles, the number of primary shoots, and a trait for characterizing the number of branching orders. Thus, our preliminary analysis resulted in the new architectural traits which were evaluated in a subsequent study. They are, plant height (correlated with branching angles), the length of the primary shoot, the number of nodes on the primary shoot, the number of primary shoots, the number of secondary shoots per primary shoot and the number of tertiary shoots per primary shoot.

2.2 Introduction

2.2.1 Rose domestication and its breeding value

Roses have great cultural importance due to their symbolic meanings. Meilland stated that “No other flower is as universally loved and grown or has a more illustrious history than the rose.” (Roberts et al., 2003). Roses have made great contributions to the world as landscape plants and, as cut flowers in the floral industry. The essential oils of roses are also commonly used in the perfume and cosmetic industries. (Bendahmane et al., 2013). The rose is a key ornamental plant in the $2.81 billion wholesale US shrub market. Garden roses contribute approximately $400 million to the wholesale US domestic bare root and container production. (AmericanHort, 2014).

Roses have been cultivated since 3,000 BC in China, western Asia and northern Africa. Wild roses were first utilized as fences to stop animals (Bendahmane et al., 2013). The Romans, Greeks, and Persians used domesticated roses as ornaments and for medicinal use. Chinese roses were introduced to Europe in 1400s, which lead to the development of ‘modern rose cultivars’ via the hybridization among Chinese, European and Middle Eastern roses (Raymond, 1999) (Figure 1). Nowadays, there are 30,000 to 35,000 rose (*Rosa* × *hybrida)* cultivars in the world (Blechert and Debener, 2005; Gudin, 2003). According to the US patent record (2010-2013), 10-20% of the roses patented in North America were miniatures or hybrid teas while 50-60% are either shrubs or floribunda roses (Byrne, 2013).

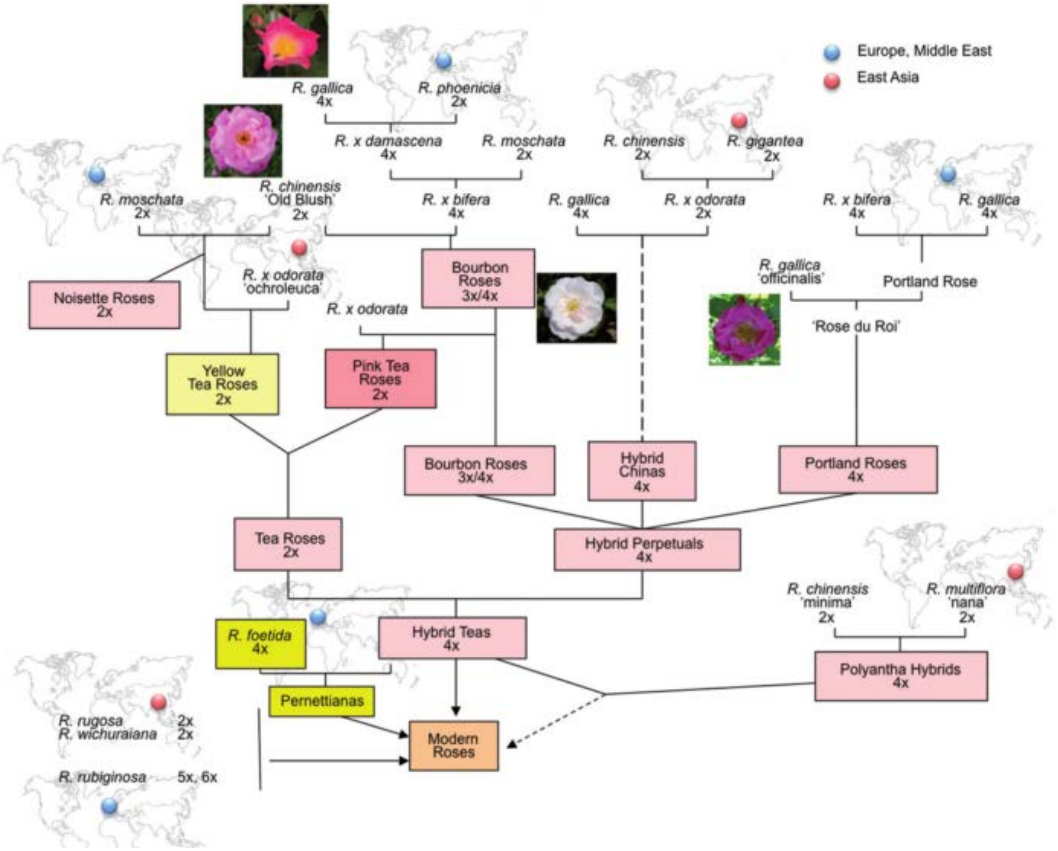


Figure 1. Schematic representation of major steps of modern rose genealogy (Raymond, 1999).

From a commercial perspective, important traits in roses include plant architecture, flower characteristics (development, architecture, and senescence), and resistance to biotic and abiotic stresses (Bendahmane et al., 2013). Currently, garden roses that can produce cut flowers with petal color evolution, glossy foliage, attractive hips after fall defoliation and vigorous growth types not needing rootstocks are attracting more and more attention from both breeders and consumers (Gudin, 2003). Other than ornamental characters, rose breeders are challenged to effectively and efficiently develop

a rose which has resistance to diseases: black spot, cercospora, powdery mildew, and rose rosette virus (Byrne, 2013; Debener and Byrne, 2014). Generally, if the commercial cultivars show adaptation to adverse environmental conditions (both biotic and abiotic stress), their aesthetic value lasts for a longer time during the growing season, which increases their market demand (Nybom, 2009).

2.2.2 Challenges of breeding and approaches to study rose traits

The present rose cultivars consist of a multispecies complex derived from intercrossing of 8-20 species. Most roses are distributed throughout the Northern Hemisphere (Krussmann, 1981), and have a wide range of ploidy levels from 2n=2x=14 to 2n=10x=70 (Roberts et al., 2009; Jian et al., 2010; Ueckert et al., 2015). Among these are the dog roses in the Caninae section which are permanent sexual pentaploids with an unusual asymmetric meiosis (Lim et al., 2005; Kovarik et al., 2008). More than half of wild rose species are polyploid (Vamosi and Dickinson, 2006). Most modern roses are diploid, triploid and tetraploid hybrids (Debener and Linde, 2009; Rajapakse et al., 2001; Ueckert et al., 2015; Zhang et al., 2006; Zlesak, et al., 2010). Although interploidy crosses are done in rose breeding and polyploid germplasm can assist in creating diverse genetic combinations, the dynamics of rose ploidy in interploidy crosses is poorly understood. In addition to polyploidy of roses, roses are predominantly outcrossing highly heterozygous, and suffer from severe inbreeding depression. The paucity of knowledge about rose genetics is a major challenge in rose breeding, which makes rose breeding mostly based on chance and experiences (Gudin, 2000). As a result, the

inheritance patterns of most morphological and physiological traits of roses are hard to predict. Thus barriers to the introgression of alleles of interest are the polyploidy and the high heterozygosity of the rose. Fortunately roses are vegetatively propagated, and thus maintaining specific genetic combinations is easy (Debener and Mattiesch, 1999; Rajapakse et al., 2001).

During the last several decades there has been consistent progress in the development of genomic tools to improve our understanding of key traits and breeding technology in rose (Byrne 2009; Debener and Byrne, 2014). Multiple flower and disease resistance traits controlled by more than 20 major genes have been mapped (Byrne, 2009), multiple linkage maps been created and BAC libraries have been constructed (Biber et al., 2010; Hess et al., 2007; Kaufmann et al., 2003). Since the early 1990s, hundreds of RFLPs, AFLPs, SSRs and other markers such as RGAs, PKs, CAPs, SCARs have been utilized to create diploid and tetraploid maps (Byrne, 2009; Gar et al., 2011; Koning-Boucoiran et al., 2012; Spiller et al., 2011; Chao Yu et al., 2014). QTLs controlling various traits including disease resistance, the related resistant gene analogs and pathogenesis resistance genes have been placed on the map (Debener and Byrne, 2014).

In 1999, the first diploid map was constructed based on mostly RAPD and AFLP markers (Debener and Mattiesch, 1999). Several years later, it was improved by adding SSR markers (Yan et al., 2005). The next map was created in a tetraploid population (Rajapakse et al., 2001). The third map was developed with AFLP markers in a diploid population derived from an interspecific cross between *R. wichurana* and a dihaploid

hybrid (Crespel et al., 2002). Dugo et al., (2005) established another mapping population derived from the hybridization of *R. wichurana* and 'Blush Noisette'. A map for diploid population 97/7 was developed in 2006, based on *R. multiflora* (Linde et al., 2006). In 2009, a map was constructed with NBS markers and SSRs in a tetraploid population for powdery mildew resistance in the Netherlands (Koning-Boucoiran et al., 2009). The first integrated consensus map (ICM) for rose was published by Spiller et al., based on four diploid populations in 2010. This map created a standard nomenclature for rose LGs, and provided location information regarding important ornamental traits, such as recurrent blooming, self-incompatibility, and black spot resistance (*Rdr1)*. It is a good tool for marker assisted selection because it integrated the information for highly relevant traits of roses. It will further assist in sequencing the whole rose genome in the future (Spiller et al., 2011). An autotetraploid linkage map was developed with AFLP, SSR markers and three morphological markers (Gar et al., 2011). Chao Yu et al., (2014) developed a tetraploid genetic linkage map for roses from AFLPs and SSRs based on a cross involving a Chinese traditional rose cultivar which may help to cover more genome regions and fill gaps within the linkage groups. With next generation sequencing and other novel technologies, the whole picture of the rose genome and important target genes will be revealed and understood better. Additionally, the designer nucleases offer a potential method of modifying rose DNA to obtain disease resistant roses (Debener and Byrne, 2014).

2.2.3 TAMU rose breeding and genetics program

The rose breeding program at Texas A&M University (TAMU) was founded in the early 1990s when Dr. Robert E. Basye, a rose breeder established the Endowed Chair in Rose Genetics to establish a Rose Breeding and Genetics Program in the Department of Horticultural Sciences to continue and expand upon the rose breeding he had been doing during his lifetime. Dr. Basye bred roses for more than 50 years in Texas aiming to obtain roses that are well adapted to the hot and humid climate of Texas. He wanted "healthy rose bushes on which to hang those beautiful flowers" (Aggie Horticulture, 2014; Texas A&M Rose Breeding and Genetics Program, 2014).

Some roses Dr. Basye released were "Belinda's Dream", "Basye's Legacy" (1966), "Basye's Purple" (1968), "Basye's Myrrh Scented Rose" (1980), and "Basye's Blueberry" (1982) (Aggie Horticulture, 2014). The most popular of these would be 'Belinda's Dream' (large pink, fragrant flowers with good disease resistance) which was designated as an "Earth-Kind" rose.

College Station is located in a warm, humid subtropical climate where roses are exposed to foliar diseases, such as black spot and cercospora. In the early stage, the research work of TAMU Rose Breeding & Genetics Program was focused on the evaluation of rose germplasm (Byrne et al., 2010), the usefulness of the amphidiploid approach of incorporating disease resistance (Ma et al., 1997; 2000), the use of markers to accelerate the breeding process (Byrne, 2007), the analysis of the diversity of Rosa using various marker systems (Kim and Byrne, 1996; Jan et al., 1999; Kiani et al., 2008; 2009) and optimizing transformation protocols for the rose (Kim et al., 2004a; 2004b).

The germplasm the TAMU rose breeding program is using for the development of disease resistant roses includes selections from Dr. Basye's work, and diploid species including *Rosa wichurana* (Byrne, 2007). In 2008, Mr. Ralph Moore who was world-renowned as the "Father of the Miniature Rose" donated his rose germplasm to the TAMU rose breeding program. This was a perfect match for Dr. Basye's legacy because, although Basye roses have good disease resistance, they do not have the diversity of ornamental traits found in the Moore germplasm. Based on this fact, the research emphasis of the rose breeding program was shifted to combine good traits from the germplasm developed by Moore and the good disease resistance from Basye and TAMU roses (Texas A&M Rose Breeding and Genetics Program, 2014). Currently, the rose breeding research program at TAMU has unreleased selections from both Basye and Moore's rose legacy.

Since the research program has germplasm including diploids, triploids and tetraploids, work on interploidy crosses is ongoing. In addition, with the rapid development of genomics, the research team collaborated with partners from South Carolina, Germany, Holland, France and Israel to develop both diploid and tetraploid maps of the rose (Rajapakse et al., 2001; Zhang et al., 2006; Spiller et al., 2010; Gar et al., 2012).

2.2.4 Plant architecture

Despite the fact that the concept of plant architecture has been widely used in studies, no universally accepted definition exists. The understanding of this concept

varies with the context. It has been used as a model to describe the growth patterns of a plant species (Hallé et al., 1978). In this case, plant architecture involves the rules determining the growth and structure of a group of individuals. Plant architecture also refers to the structural expression of the growth process of a specific individual. In this context, “plant architecture” demonstrates the 3D structure of a plant with topological and geometrical traits (e.g. orthotropic (vertical shoot orientation, with radial leaf arrangement) vs. plagiotropic (horizontal shoot orientation, with planar leaf arrangement) traits). Ross (1981) proposed a similar explanation for plant architecture, which is “a set of features delineating the shape, size, geometry and external structure of a plant”, or “for the parts of the plant that are above ground, it includes the branching pattern, as well as the size, shape and position of leaves and flower organs.” This concept was also used in other research fields of plants, e.g. hydraulics (Zimmermann, 1978; Tyree, 1991), plant growth modelling (de Reffye, 1997) plant measurement (Smith, 1984; Sinoquet, 1997), and in carbon partitioning (Perttunen, 1996).

The formation of plant architecture starts from bud fate, which determines the positioning and number of shoots. The initiation period determines the expansion and orientation of leaves and internodes, and floral transition determines the number of flowers and bloom period. Additionally, stems along with leaves determine the shape and growth type of plant, which is very important for aesthetic quality (Boumaza et al., 2009).

Plant architecture is useful in the identification of plant species. It can greatly influence the cultivation of a plant and its yield, hydraulic efficiency (McCulloh et al.,

2005), leaf-display efficiency (Pearcy et al., 2005) and disease resistance (Ando et al., 2007). One of the great successes of the Green Revolution, which largely increased the productivity of crops and was based on the modification of plant architecture, wheat varieties with shorter and sturdier stems tend to yield more as they are less likely to lodge due to wind and rain stress (Peng et al., 1999).

2.2.5 Methods for characterizing plant architecture

The phenotyping of plant architecture is labor-intensive and time-consuming. Plant architecture can be broken into traits: axes and metamers, where a metamer is the unit consisting of an internode, a node, its axillary bud and a leaf (White, 1979). Axes and metamers could be "morphologically (length, diameter, etc.), topologically (order of branching, etc.), and geometrically (branching angle, etc.)" described. (Godin, 1999). Plant architecture analysis was done on trees such as walnut (Barthélémy et al., 1995) and birch (Caraglio, 1996) first. And then on rose by Morel et al. (2009) and Crespel et al. (2014).

Based on the descriptions above, a representation of plant architecture should include:

• Decomposition information, which refers to the way different traits form a whole plant;

• Geometrical information, referring to the shapes and positioning of the traits. The traits are independent one from another;

• Topological information, which refers to the hierarchical relationship among the traits within the branching system.

Plant architecture results from the growth and branching processes and thus can be objectively characterized, by the length and diameter of the entities (morphologically), by determining the way they are connected (succession and branching), and by characterizing their orientation in space (i.e., shoot angles) (Godin et al., 1999a).

2.2.6 Objectives

The goal of this study was to evaluate the variation of 19 plant architectural traits in diploid rose populations in order to select the best representing traits of plant architecture. Four rose populations in the field were characterized for 19 architectural traits in this preliminary study.

2.3 Materials and methods

2.3.1 Plant materials

Diploid rose populations (Table 1) were derived from the hybridization of rose parents with a range of plant architecture ‘J06-20-14-3’, ‘M4-4’, ‘Old Blush’, ‘Sweet Chariot’, ‘Vineyard Song’, ‘Red Fairy’, ‘Little Chief’, ‘J06-30-3-3’, and ‘J06-30-3-6’ from 2010-2012 (Figures 2 and 3). The four F_1 rose populations used for the preliminary study included the families ‘OdBsM4’ (Old Blush × M4-4), ‘SwChM4’ (Sweet Chariot × M4-4), ‘J20VySg’ (J06-20-14-3 × Vineyard Song) and ‘J20SwCh’ (J06-20-14-3 ×

Sweet Chariot) (Table 2, Figure 2). Ten seedlings in each population were selected to be evaluated for plant architecture. Segregation of architectural traits was seen among ten seedlings in each population. Measurements were made on three shoots that grown from base of the plant per seedling.

Growth type of our rose parents ranges from ground cover/ climbing (slightly raised stems close to the ground but not fully climbing), climbing (stems reaching outwards and upwards often bending back towards the ground), intermediate (shoots not fully extending upright), to completely upright (Figure 3) (Jones, 2013).

Table 1. Diploid rose families evaluated in preliminary study.

FP[1]	**MP[2]**	**Population size (phenotyped number)**	**Family**	**Cross year**
J06-20-14-3	Sweet Chariot	57 (10)	J20SwCh	2010
J06-20-14-3	Vineyard Song	93 (10)	J20VySg	2010
Sweet Chariot	M4-4	118 (10)	SwChM4	2010
Old Blush	M4-4	18 (10)	OdBsM4	2010

[1] Female parent
[2] Pollen parent

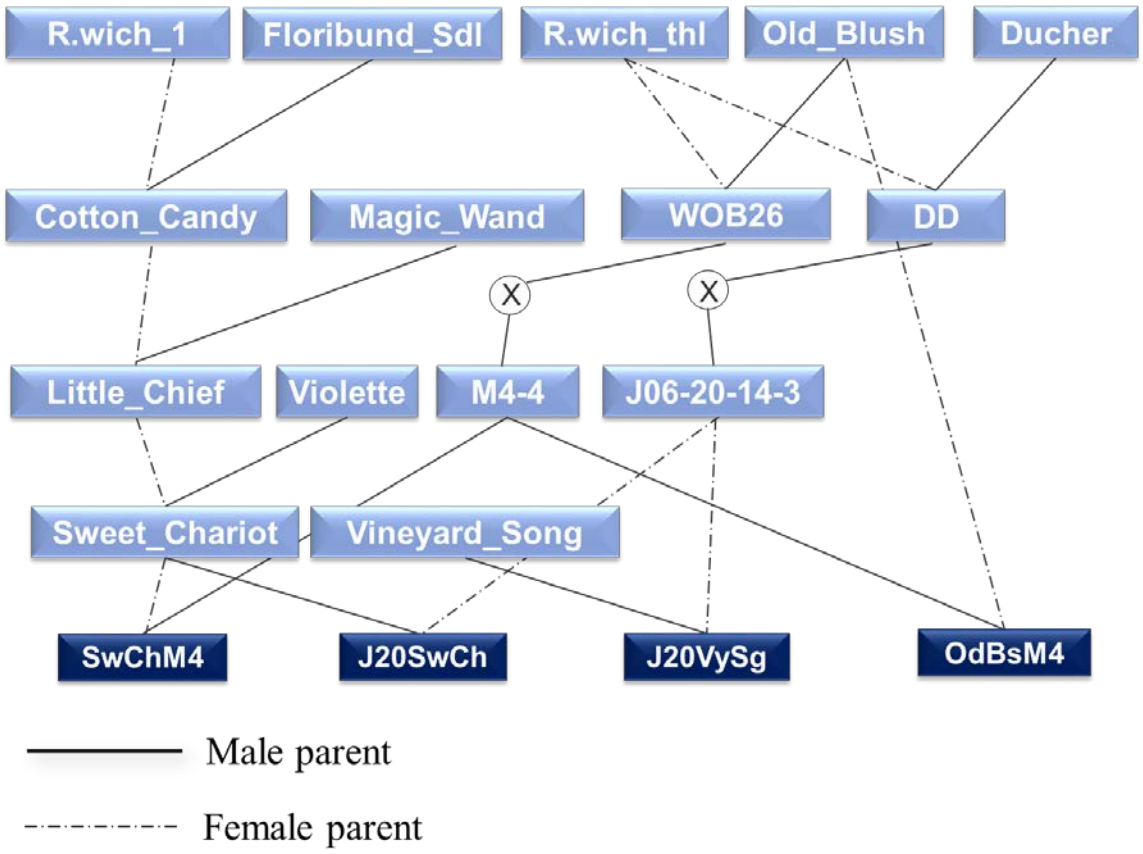


Figure 2. Pedigree diagram of four rose populations in the preliminary research on rose plant architecture.

Table 2. Growth types of various diploid roses.

Parents	**Growth types**
Rosa. wichuriana'Basye's thornless'	Ground cover/Climbing bush
Old Blush	Upright bush
J06-30-3-3	Intermediate
Sweet Chariot	Upright bush
J06-30-3-6	Ground cover/Climbing bush
Vineyard Song	Climbing bush
M4-4	Climbing bush
Little Chief	Intermediate
J06-20-14-3	Intermediate
Red Fairy	Intermediate

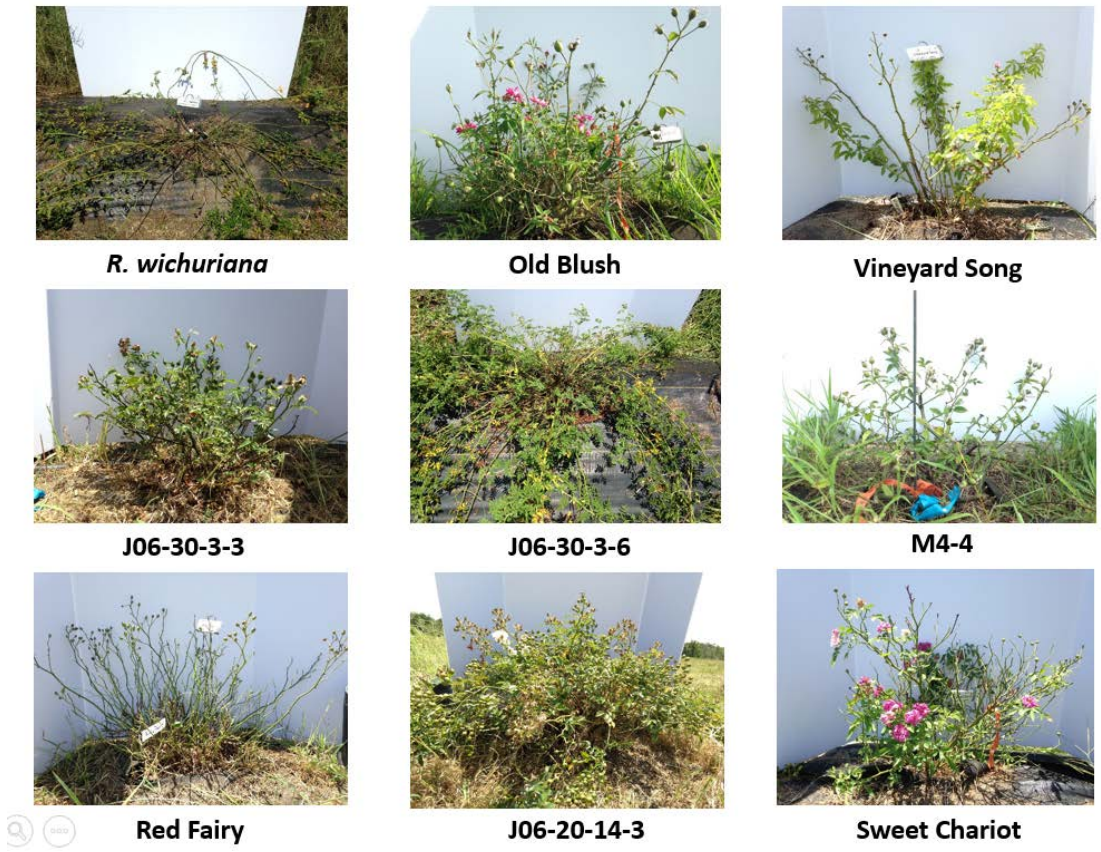


Figure 3. Growth type of various diploid roses.

2.3.2 Field experiment and trait assessment

The seedlings of four diploid populations in this study were planted in double rows at 1 m × 1 m × 3.5 m spacing. The field is located two miles from Texas A&M University in College Station. The soil in this field belongs to the unit "Zack-Boonville-Zulch" (Figure 4 and Soil survey of Brazos County, Texas), which is dark brown, strongly acid fine sandy loam. Our site is marked by the red star in Figure 4. The main problem with this type of soil is low fertility, drought, poor drainage due to a claypan

and a severe hazard of erosion. The individual plants were planted in rows oriented east to west in an open field that receives full sun. Raised beds were constructed in the field and black ground cloth was used for weed control. The irrigation was applied as needed without the application of fungicides or pesticides during the evaluation. Pruning to remove dead tissue and synchronize the growth of the seedlings was conducted in March. Each genotype is represented by one plant in the field. The preliminary evaluation for plant architecture was done in the field in spring (May) 2014. The climate is a humid subtropical climate (Table 3, National Weather Service, 2014). The latitude of the location is 30.6504 North and the longitude of it is -96.3226. Plant architecture data consisted of qualitative and quantitative traits of growth, branching and the flowering process.

Table 3. Monthly temperature and precipitation of 2014 in College Station, TX (National Weather Service, 2014)

	Maximum (°C)	**Minimum (°C)**	**Mean**	**Total precipitation (mm)**
January	15.3	2.1	8.7	33
February	16.8	5.6	10.3	11
March	19.8	7.7	13.8	41
April	25.7	14.4	20.1	31
May	28.8	17.3	23.1	229
June	32.7	23.3	28.0	41
July	33.8	23.1	28.4	171
August	34.8	23.7	29.2	10
September	32.2	21.7	27.0	167
October	28.4	16.3	22.3	46
November	18.8	7.4	13.1	150
December	17.1	8.4	12.8	65

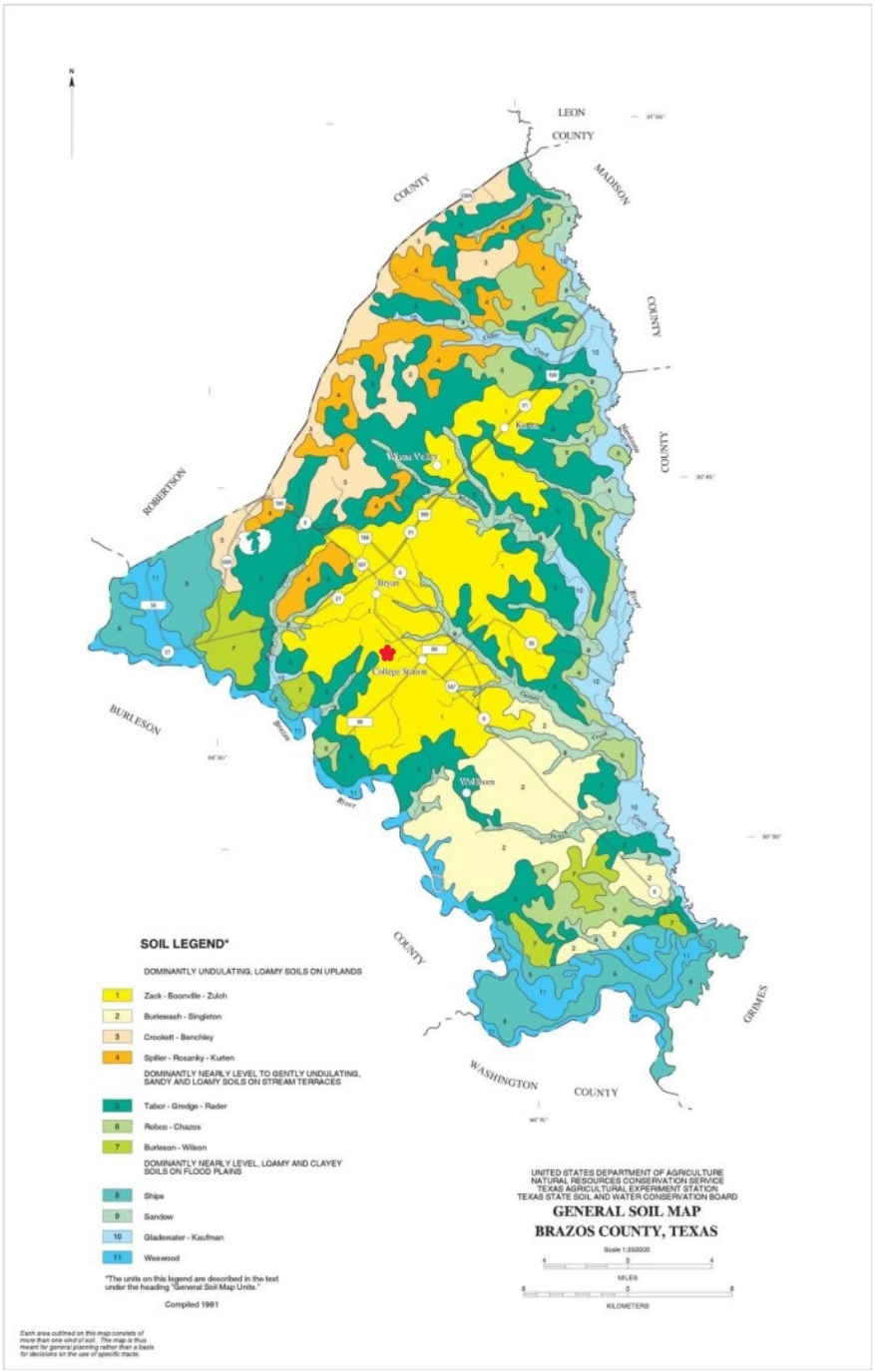


Figure 4. General soil map of Brazos County, TX (General Soil Map, Brazos County, Texas Side: 1 of 1 < https://texashistory.unt.edu/ark:/67531/metapth130277/m1/1/>).

2.3.3 Measurements of the traits of plant architecture

Plant architecture was characterized based on four categories, vegetative traits, reproductive traits, shoot traits and branching angles. Plant architecture was divided into the following traits: the number of nodes on the vegetative part and reproductive part, and the shoot of primary (1st order) and secondary (2nd order) shoots, respectively (Figure 5 and 6); the length of vegetative, reproductive parts and the shoot of primary and secondary shoots, respectively (Figure 5 and 6); the internode length of primary and secondary shoots (Figure 5), the branching angles between primary and secondary shoots, and those between secondary (2nd order) and tertiary (3rd order) shoots (Figure 7); inflorescence characteristics including the number of flowers on the terminal inflorescence on the primary and secondary shoots and inflorescence structure type (Figure 8).

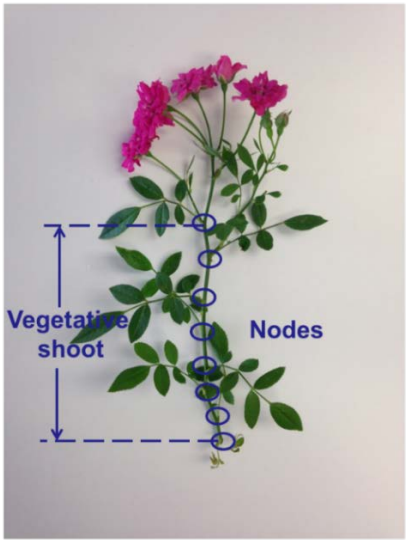


Figure 5. Traits (number, length of nodes and internode length) on the vegetative part of rose.

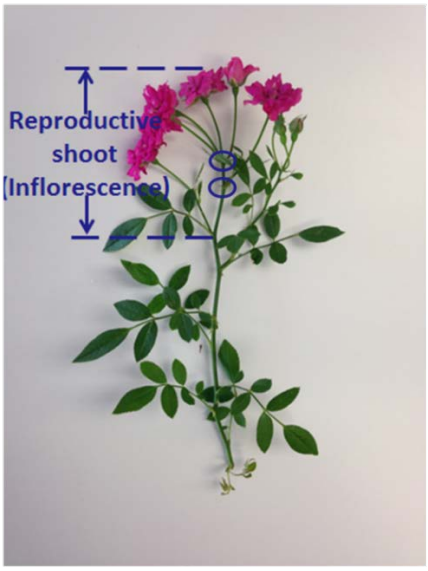


Figure 6. Traits (number, length of nodes) on the reproductive part of rose and the number of flowers on the terminal inflorescence.

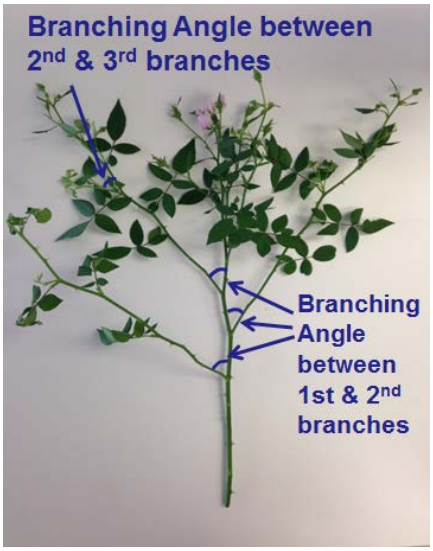


Figure 7. Branching angles on rose.

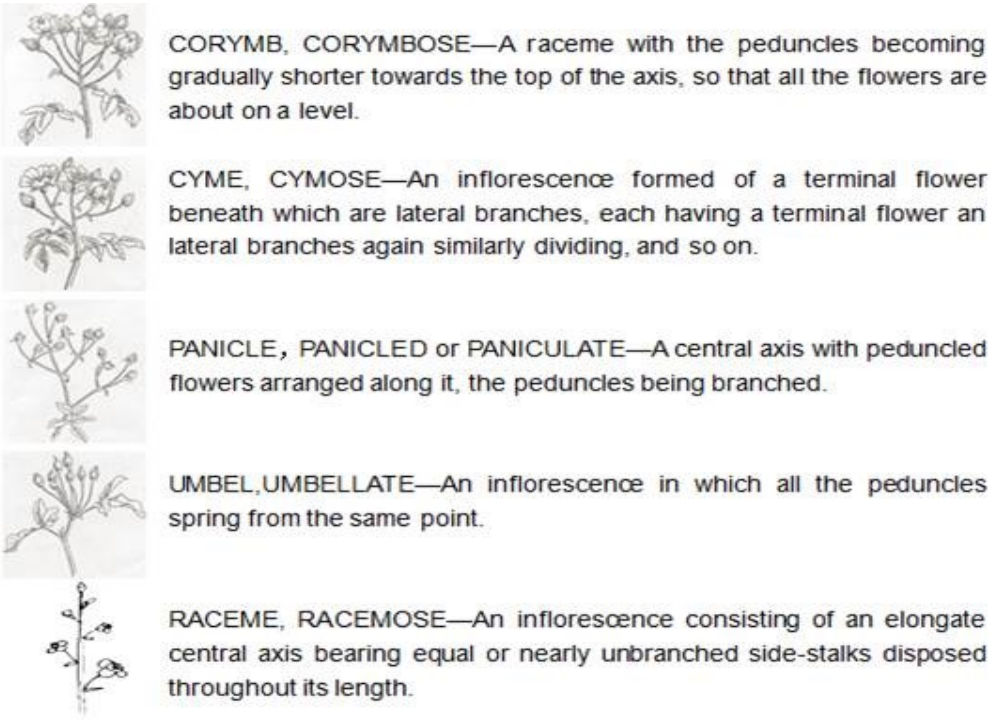


Figure 8. Inflorescence types in Rosa flowers (The Genus Rosa, Ellen Willmott, 1914).

2.3.4 Statistical analysis

The statistical analysis of the phenotypic data, analysis of variance (ANOVA), correlation analysis and principal component analysis were carried out using JMP software, version 12.0. A multivariate model based on 18 architectural traits was used to estimate phenotypic correlations. Correlations were computed on a pair-wise basis for all traits. Correlation estimate of $r \geq 0.65$ was considered strong to very strong; a correlation estimate r between 0.50 and 0.64 was considered moderate; a correlation estimate r between

0.30 and 0.49 was considered weak.

2.4 Results

2.4.1 Results of ANOVA

One-way ANOVA comparing means of architectural traits among families revealed significant differences in most of the architectural traits measured among families (Table 4).

The number of nodes on the vegetative part differed among the four populations on both primary and secondary shoots (Tables 4 and 5). The “Old Blush × M4-4” family had the lowest number of nodes on the primary (8.4) and secondary vegetative part (6.4). The “J06-20-14-3 × Vineyard Song” family had the highest number of nodes on the primary vegetative part (17.7), whereas the “Sweet Chariot × M4-4” family had the highest number of nodes (10.0) on the secondary shoot of the vegetative part (Table 5).

The four families differed for the length of the primary vegetative part (Tables 4 and 6). The “Old Blush × M4-4” family had the shortest primary vegetative part (22.5cm), while the “J06-20-14-3 × Vineyard Song” family had the longest primary vegetative part (41.9cm) (Table 6).

Although the vegetative parts varied in both the number of nodes and the length for both orders, the internode length was uniform among the families studied (Tables 4 and 7).

The number of inflorescence nodes differed among the four populations on both

primary and secondary shoots (Tables 4 and 8). Consistent with the number of nodes on vegetative parts, the “Old Blush × M4-4” family had the lowest number of inflorescence nodes on the primary (2.4) and secondary shoots (1.8). The family that had the most inflorescence nodes on both primary (4.7) and secondary (4.4) shoots was “J06-20-14-3 × Sweet Chariot” (Table 8).

The length of the reproductive shoot and the number of nodes on the branch, (Tables 4, 9 and 10) also differed among the families. The family with the shortest reproductive shoots and the least nodes was the “Old Blush × M4-4” family. The family with the longest primary reproductive shoot was the “J06-20-14-3 × Sweet Chariot” family (9.8cm), while the longest secondary reproductive shoot was in the “J06-20-14-3 × Vineyard Song” family (7.3cm) (Table 9). The family with the most nodes on the primary branch was the “J06-20-14-3 × Vineyard Song” family (21.8), while the family with the most nodes on the secondary branch was the ‘Sweet Chariot × M4-4’ family (13.8) (Table 10).

The four families differed for the length of the primary shoot (Tables 4 and 11). The “Old Blush × M4-4” family had the shortest primary shoot (29.1cm), while the “J06-20-14-3 × Vineyard Song” family had the longest primary shoot (50.3cm) (Table 11).

The number of flowers on the terminal inflorescence of both primary and secondary shoots differed among families (Tables 4 and 12), with the “Old Blush × M4-4” family having the fewest flowers on both order level shoots (9.2/6.8), the “J06-20-14-3 × Vineyard Song” family had the most flowers on the primary inflorescence (25.5),

and the "J06-20-14-3 × Sweet Chariot" family had the most flowers on the secondary inflorescence (19.4) (Table 12).

The branching angles between the primary and the secondary shoots did not differ among families but those between the secondary and the tertiary shoots did (Tables 4 and 13). "J06-20-14-3 × Sweet Chariot" was characterized by the widest branching angle (59.0˚) and "Sweet Chariot × M4-4" was characterized by the narrowest branching angle between secondary and tertiary shoots (42.5˚) (Table 13).

Table 4. Summary of One-way ANOVA comparing means of architectural traits of four families and range (in parenthesis).

Traits	**Primary shoot**	**Secondary shoot**
Number of nodes on vegetative part	***	**
	(5-36)	(3-14)
Length of vegetative part (cm)	***	NS
	(13-66)	(6-30)
Number of inflorescence nodes	**	***
	(1-7)	(1-6)
Length of reproductive part (cm)	***	*
	(4-12)	(4-11)
Number of nodes on the shoot	***	***
	(6-39)	(4-17)
Length of the shoot (cm)	**	NS
	(17-73)	(9-39)
Number of flowers on terminal inflorescence	***	***
	(1-37)	(3-31)
Internode length (cm)	NS	NS
	(0.7-4.3)	(0.9-4.6)
Branching angles	(1^{st}&2^{nd} shoot) NS	(2^{nd}&3^{rd} shoot) **
	(30˚-80˚)	(25˚-75˚)

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

Table 5. The number of nodes on the vegetative part for four diploid rose families.

Populations	Primary shoot	Secondary shoot
Old Blush × M4-4	8.4 b	6.4 b
Sweet Chariot × M4-4	11.4 b	10.0 a
J06-20-14-3 × Vineyard Song	17.7 a	6.7 b
J06-20-14-3 × Sweet Chariot	10.4 b	8.0 b
Significance	***	**
R^2	0.36	0.33
n	40	40

NS, *, **, *** Non-significant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively and levels not connected by same letter are significantly different.

Table 6. The length of the vegetative part for four diploid rose families (cm).

Populations	Primary shoot	Secondary shoot
Old Blush × M4-4	22.5 c	14.6 b
Sweet Chariot × M4-4	34.1 ab	20.6 a
J06-20-14-3 × Vineyard Song	41.9 a	17.0 ab
J06-20-14-3 × Sweet Chariot	25.4 bc	18.6 ab
Significance	***	NS
R^2	0.36	0.14
n	40	40

NS, *, **, *** Non-significant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively and levels not connected by same letter are significantly different.

Table 7. The internode length for four diploid rose families (cm).

Populations	Primary shoot	Secondary shoot
Old Blush × M4-4	2.7 a	2.3 a
Sweet Chariot × M4-4	3.0 a	2.1 a
J06-20-14-3 × Vineyard Song	2.7 a	2.6 a
J06-20-14-3 × Sweet Chariot	2.5 a	2.3 a
Significance	NS	NS
R^2	0.40	0.16
n	40	40

NS, *, **, *** Non-significant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively and levels not connected by same letter are significantly different.

Table 8. The number of inflorescence nodes for four diploid rose families.

Populations	Primary shoot	Secondary shoot
Old Blush × M4-4	2.4 b	1.8 b
Sweet Chariot × M4-4	3.8 a	3.7 a
J06-20-14-3 × Vineyard Song	4.1 a	3.9 a
J06-20-14-3 × Sweet Chariot	4.7 a	4.4 a
Significance	**	***
R^2	0.28	0.52
n	40	40

NS, *, **, *** Non-significant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively and levels not connected by same letter are significantly different.

Table 9. The length of the reproductive part for four diploid rose families (cm).

Populations	Primary shoot	Secondary shoot
Old Blush × M4-4	6.6 c	5.5 b
Sweet Chariot × M4-4	8.5 ab	6.9 ab
J06-20-14-3 × Vineyard Song	8.4 b	7.3 a
J06-20-14-3 × Sweet Chariot	9.8 a	7.2 a
Significance	***	*
R^2	0.39	0.18
n	40	40

NS, *, **, *** Non-significant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively and levels not connected by same letter are significantly different.

Table 10. The number of nodes on the shoot for four diploid rose families.

Populations	Primary shoot	Secondary shoot
Old Blush × M4-4	10.8 b	8.2 c
Sweet Chariot × M4-4	15.2 b	13.8 a
J06-20-14-3 × Vineyard Song	21.8 a	10.6 b
J06-20-14-3 × Sweet Chariot	15.1 b	12.4 ab
Significance	***	***
R^2	0.40	0.46
n	40	40

NS, *, **, *** Non-significant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively and levels not connected by same letter are significantly different.

Table 11. The length of the shoot for four diploid rose families (cm).

Populations	Primary shoot	Secondary shoot
Old Blush × M4-4	29.1 c	20.1 b
Sweet Chariot × M4-4	42.7 ab	27.5 a
J06-20-14-3 × Vineyard Song	50.3 a	24.2 ab
J06-20-14-3 × Sweet Chariot	35.2 bc	25.8 ab
Significance	**	NS
R^2	0.36	0.16
n	40	40

NS, *, **, *** Non-significant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively and levels not connected by same letter are significantly different.

Table 12. The number of flowers on the terminal inflorescence for four diploid rose families.

Populations	Primary shoot	Secondary shoot
Old Blush × M4-4	9.2 b	6.8 c
Sweet Chariot × M4-4	21.9 a	12.2 b
J06-20-14-3 × Vineyard Song	25.5 a	14.9 ab
J06-20-14-3 × Sweet Chariot	23.2 a	19.4 a
Significance	***	***
R^2	0.39	0.41
n	40	40

NS, *, **, *** Non-significant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively and levels not connected by same letter are significantly different.

Table 13. Branching angles for four diploid rose families.

Populations	Primary & Secondary	Secondary & Tertiary
Old Blush × M4-4	54.5 a	52.5 a
Sweet Chariot × M4-4	61.5 a	42.5 b
J06-20-14-3 × Vineyard Song	56.0 a	58.0 a
J06-20-14-3 × Sweet Chariot	50.5 a	59.0 a
Significance	NS	**
R^2	0.10	0.32
n	40	40

NS, *, **, *** Non-significant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively and levels not connected by same letter are significantly different.

2.4.2 Results of correlation analysis

Pearson correlation coefficients between phenotypic architectural traits indicated that among the 153 pairs evaluated, nine correlations were high ($r \geq 0.65$), 14 were moderate ($0.64 \geq r \geq 0.50$) and 41 correlations were weak ($0.49 \geq r \geq 0.30$) (Tables 14-17).

The conclusions based on correlation coefficients between variables could be categorized into two groups. Correlations of the same architectural traits on different order level shoots, and correlations between different architectural traits.

Correlations of the same architectural traits on the different order level shoots were evident for the number of nodes on the reproductive part ($r = 0.78$), the length of the reproductive part ($r = 0.61$), the internode length ($r = 0.54$) and the number of flowers

on the terminal inflorescence (r = 0.77) (Tables 14 and 17).

As for different architectural traits, the number of nodes on the primary vegetative part was highly correlated with the number of nodes on the primary part (r = 0.97), and moderately correlated with the length of the primary vegetative part (r = 0.50). The number of nodes on the secondary vegetative part was highly correlated with the number of nodes on the secondary shoot (r = 0.90) and the length of the secondary vegetative part (r = 0.69). It was moderately correlated with the length of secondary shoot (r = 0.63) (Table 15).

The number of inflorescence nodes on the primary shoot was moderately correlated with the length of both primary (r = 0.51) and secondary (r = 0.55) reproductive parts. The number of inflorescences nodes on the secondary shoot was moderately correlated with the number of nodes on the secondary shoot (r = 0.61), and the length of primary and secondary reproductive parts (r = 0.59 and 0.55) (Table 15).

The number of nodes on the primary shoot was moderately correlated with the length of the primary vegetative part (r = 0.52) and the length of the primary shoot (r = 0.52). The number of nodes on the secondary shoots was moderately correlated with the length of the secondary vegetative part (r = 0.69), the length of secondary shoot (r = 0.68) and the number of flowers on the primary terminal inflorescence (r = 0.50) (Table 15).

The length of the primary vegetative part was highly correlated with the length of primary shoot (r = 0.99). The length of the secondary vegetative part was highly correlated with the length of secondary shoot (r = 0.98) (Table 16).

The length of the primary reproductive part was moderately correlated with the length of secondary shoot (r = 0.50). The length of the secondary reproductive part was moderately correlated with the length of secondary shoot (r = 0.64) (Table 16).

The number of flowers on the terminal inflorescence of the primary shoot was moderately correlated with the number of nodes on the secondary shoot (r = 0.50) and highly correlated with the number of flowers on the terminal inflorescence of the secondary shoot (r = 0.77) (Table 17)

Table 14. Correlations of same traits on different order levels.

#Nodes on reproductive	Length of reproductive	Internode length	#Flowers
0.78	0.61	0.54	0.77

Table 15. Pearson correlation coefficients of architectural traits concerning the number of nodes versus other traits of seedlings from four diploid rose families.

	#Node 1st Veg	#Node 2nd Veg	#Node 1st Rep	#Node 2nd Rep	#Node 1st	#Node 2nd	Length 1st Veg	Length 2nd Veg	Length 1st Rep	Length 2nd Rep	Length 1st	Length 2nd	Internode 1st	Internode 2nd	#flw 1st	#flw 2nd	Δ1&2	Δ2&3
Length 1st Veg	**0.50**	0.12	0.19	0.23	**0.52**	0.20	1.00	0.22	0.29	0.35	**0.99**	0.27	0.47	0.22	0.38	0.23	0.11	0.11
Length 2nd Veg	0.12	**0.69**	0.26	0.30	0.18	**0.69**	0.22	1.00	0.40	0.46	0.26	**0.98**	0.13	0.43	0.24	0.25	0.10	0.10
Length 1st Rep	0.07	0.26	**0.51**	**0.59**	0.20	0.48	0.29	0.40	1.00	**0.61**	0.42	**0.50**	0.21	0.29	0.40	0.38	0.01	0.16
Length 2nd Rep	0.18	0.13	**0.55**	**0.55**	0.31	0.35	0.35	0.46	**0.61**	1.00	0.42	**0.64**	0.19	0.43	0.31	0.31	-0.05	0.24
Length 1st	0.49	0.15	0.25	0.30	**0.52**	0.25	**0.99**	0.26	0.42	0.42	1.00	0.33	0.47	0.25	0.42	0.27	0.11	0.13
Length 2nd	0.14	**0.63**	0.36	0.39	0.23	**0.68**	0.27	**0.98**	**0.50**	**0.64**	0.33	1.00	0.16	0.48	0.28	0.29	0.07	0.14
Internode 1st	-0.41	-0.24	0.07	-0.05	-0.37	-0.22	0.47	0.13	0.21	0.19	0.47	0.16	1.00	**0.54**	-0.07	-0.08	-0.01	-0.06
Internode 2nd	-0.14	-0.33	0.19	0.13	-0.08	-0.20	0.22	0.43	0.29	0.43	0.25	0.48	**0.54**	1.00	-0.12	-0.04	-0.14	0.20

Table 16. Pearson correlation coefficients of architectural traits concerning the length of part/shoot versus other traits of seedlings from four diploid rose families.

	#Node 1st Veg	#Node 2nd Veg	#Node 1st Rep	#Node 2nd Rep	#Node 1st	#Node 2nd	Length 1st Veg	Length 2nd Veg	Length 1st Rep	Length 2nd Rep	Length 1st	Length 2nd	Internode 1st	Internode 2nd	#flw 1st	#flw 2nd	Δ1&2	Δ2&3
#Node 1st Veg	1.00	0.25	0.11	0.24	**0.97**	0.31	**0.50**	0.12	0.07	0.18	0.49	0.14	-0.41	-0.14	0.41	0.23	0.12	0.22
#Node 2nd Veg	0.25	1.00	0.12	0.21	0.27	**0.90**	0.12	**0.69**	0.26	0.13	0.15	**0.63**	-0.24	-0.33	0.39	0.27	0.24	-0.08
#Node 1st Rep	0.11	0.12	1.00	**0.78**	0.36	0.45	0.19	0.26	**0.51**	**0.55**	0.25	0.36	0.07	0.19	0.35	0.39	0.19	0.13
#Node 2nd Rep	0.24	0.21	**0.78**	1.00	0.43	**0.61**	0.23	0.30	**0.59**	**0.55**	0.30	0.39	-0.05	0.13	0.43	0.45	0.13	0.09
#Node 1st	**0.97**	0.27	0.36	0.43	1.00	0.41	**0.52**	0.18	0.20	0.31	**0.52**	0.23	-0.37	-0.08	0.47	0.32	0.16	0.24
#Node 2nd	0.31	**0.90**	0.45	**0.61**	0.41	1.00	0.20	**0.69**	**0.48**	0.35	0.25	**0.68**	-0.22	-0.20	**0.50**	0.42	0.25	-0.02

Table 17. Pearson correlation coefficients concerning the number of flowers on the inflorescence and branching angles versus other traits of seedlings from four diploid rose families.

	#Node 1st Veg	#Node 2nd Veg	#Node 1st Rep	#Node 2nd Rep	#Node 1st	#Node 2nd	Length 1st Veg	Length 2nd Veg	Length 1st Rep	Length 2nd Rep	Length 1st	Length 2nd	Internode 1st	Internode 2nd	#flw 1st	#flw 2nd	Δ1&2	Δ2&3
#flw 1st	0.41	0.39	0.35	0.43	0.47	**0.50**	0.38	0.24	0.40	0.31	0.42	0.28	-0.07	-0.12	1.00	**0.77**	0.09	0.15
#flw 2nd	0.23	0.27	0.39	0.45	0.32	0.42	0.23	0.25	0.38	0.31	0.27	0.29	-0.08	-0.04	**0.77**	1.00	-0.07	0.24
Δ1&2	0.12	0.24	0.19	0.13	0.16	0.25	0.11	0.10	0.01	-0.05	0.11	0.07	-0.01	-0.14	0.09	-0.07	1.00	-0.01
Δ2&3	0.22	-0.08	0.13	0.09	0.24	-0.02	0.11	0.10	0.16	0.24	0.13	0.14	-0.06	0.20	0.15	0.24	-0.01	1.00

2.4.3 Results of principal component analysis

The principal components 1, 2, and 3 of the PCA accounted for 34.5%, 15.2%, and 12.7% of the variability, respectively and so together 62.4% of the total variability. The four most important variables that made up the three principal components included the length of the secondary reproductive part which accounted for 7.8% of the total variability, the length of the primary reproductive part which accounted for 6.6% of the total variability, the internode length of the secondary shoot which accounted for 6.1% of the total variability, and the number of nodes on the secondary shoot which accounted for 4.6% of the total variability (Table 18).

Table 18. The important variables that made up three principal components and their importance within each principal component.

	Important variable 1		**Important variable 2**		**Important variable 3**		**Important variable 4**	
	Variable	**%**	**Variable**	**%**	**Variable**	**%**	**Variable**	**%**
Principal component 1	Length of 2nd reproductive part	16.6	Length of 1st reproductive part	15.0	Internode of 2nd shoot	14.1	#Nodes on 2nd shoot	10.0
Principal component 2	Length of 2nd reproductive part	13.6	#Nodes on 2nd vegetative part	10.3	Length of 1st reproductive part	9.3	Internode of 2nd shoot	7.9
Principal component 3	#Nodes on 2nd vegetative part	13.2	Internode of 1st shoot	12.3	#Nodes on 2nd shoot	9.3	#Nodes on 1st vegetative part	6.1

Among the important variables that made up three principal components, the length of the primary reproductive part was moderately correlated with the length of the secondary reproductive part (r = 0.61) (Table 19).

Table 19. Correlations between the important variables that made up three principal components.

	#Nodes on 2nd shoot	**Length of 1st rep part**	**Length of 2nd rep part**	**Internode of 2nd shoot**
#Nodes on 2nd shoot	1.0			
Length of 1st rep part	0.48	1.0		
Length of 2nd rep part	0.35	**0.61**	1.0	
Internode of 2nd shoot	-0.20	0.29	0.43	1.0

2.4.4 Flower inflorescence type

There are five common inflorescence structure types in Rosa flowers (Willmott, 1914). Namely, corymb (corymbose), cyme (cymose), panicle (panicled or paniculate), umbel (umbellate) and raceme (racemose) (Figure 8). Most common inflorescence structure type seen among rose seedlings is a cyme, or paniculiform cyme (looks like panicle but the oldest flower is at the tip of the shoots) (Figures 9 and 10) (“Inflorescence Types.pdf” n.d.). The number of pedicels observed per peduncle (a

pedicel is a stem that attaches a single flower to the inflorescence.) varied from one to four. Reversed raceme or false raceme was observed among the rose seedlings (Gray, 1887) (Figure 11). Mixed inflorescence structure types (cyme and (reversed) raceme) were also observed on the rose parent ‘Old Blush’ (Figure 12) and some of the rose seedlings. Solitary flowers were found in some rose seedlings (Figure 13). Additionally, rose seedlings with unknown inflorescence types were also observed. In these the form of the inflorescence is a panicle, but the florets on the terminal inflorescence are of different ages and therefore, whether the inflorescence is determinate or indeterminate is unknown (Figure 14a, b) Indeterminate inflorescence is defined as “species produce an inflorescence meristem that only generates floral meristem from its periphery.” (Bradley, et al., 1997). In other words, the apical meristem of the terminal bud from which the inflorescence is initiated remains active (indefinite growth) as the inflorescence develops, the oldest flowers or buds are those located farthest from the terminal bud, or at the base or outside of the inflorescence (“Inflorescence Types.pdf” n.d.). A typical type of indeterminate inflorescence is a raceme. Determinate inflorescence is defined as “the inflorescence meristem is eventually converted to a floral identity, resulting in the production of a terminal flower” (Bradley, et al., 1997) Therefore, the oldest flower is located at the end of the stem or in the center of the inflorescence A typical type of determinate inflorescence is cyme (“Inflorescence Types.pdf” n.d.).

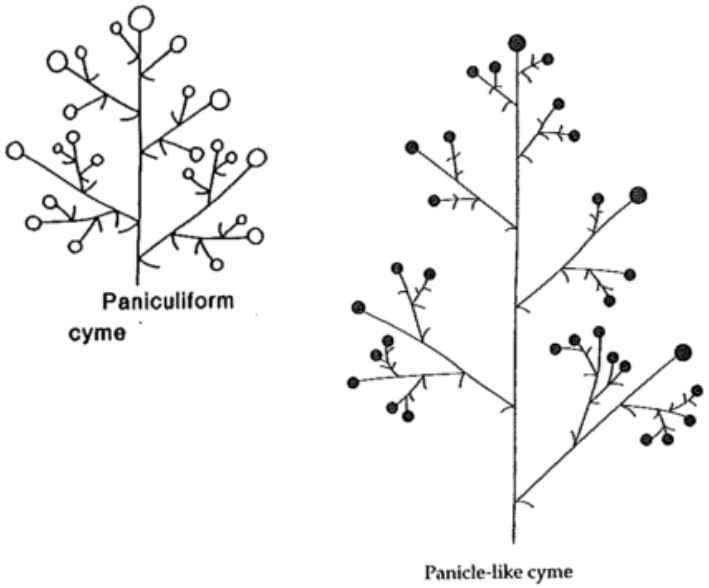


Figure 9. Paniculiform cyme inflorescence (“Inflorescence Types.pdf” n.d. <http://bpp.oregonstate.edu/files/bpp/webfm/pdf/bot425/inflorescence%20types.pdf>).

Figure. 10. Paniculiform cyme inflorescence observed among rose seedlings.

Figure 11. Reversed raceme flower inflorescence observed among rose seedlings.

Figure 12. Mixed inflorescence types (Left: raceme; Right: cyme) observed on the rose parent ‘Old Blush’.

Figure 13. Solitary flower observed among rose seedlings.

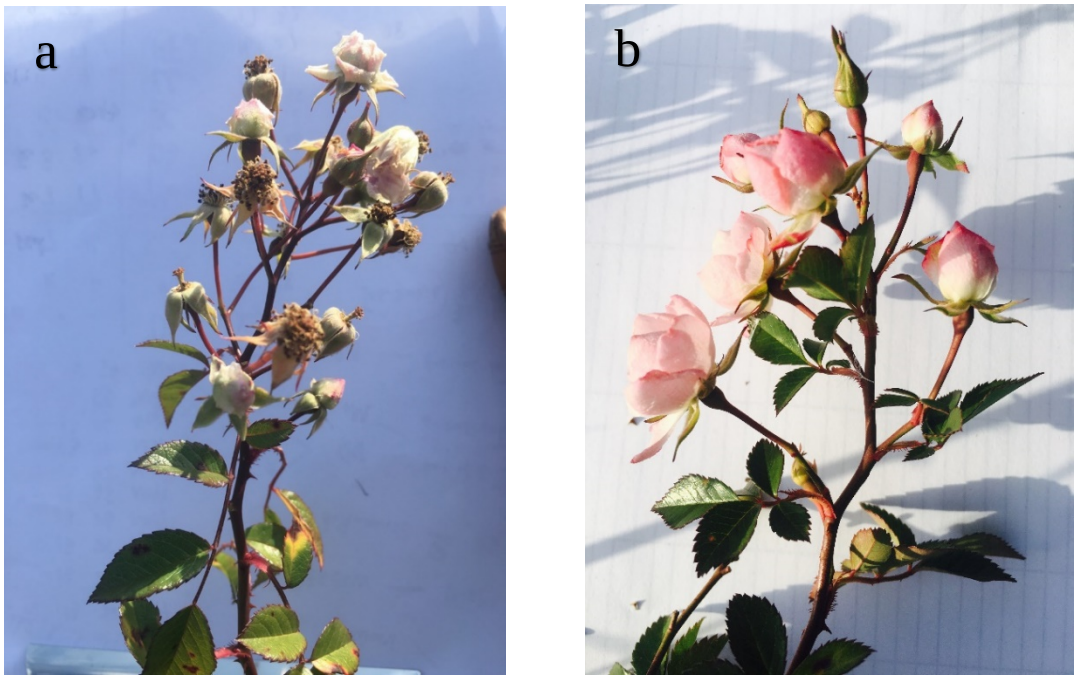


Figure 14a & b. Terminal inflorescences with unknown inflorescence type observed among rose seedlings.

Table 20. Summary of types of inflorescences and number of rose seedlings of each type.

Type of inflorescence	Number of seedlings
Cyme	13
Cyme + Reversed raceme	9
Reversed raceme + Solitary flower	4
Reversed raceme	6
Solitary flower	2
Cyme + Solitary flower	2
Raceme	2
Unknown	2

2.5 Discussions and conclusions

Plant architecture is description based on the decomposition of the plant into traits, specifying their biological type, their shape, their location/orientation in space and/or the way these traits are physically related with one another (Godin, 2000). To describe plant architecture of roses, we propose characterizing it on the basis of its growth (vegetative and reproductive) and branching processes.

Based on the result of ANOVA (Table 4-13), the four rose families differed among each other in all the traits of rose plant architecture in our preliminary study except for the length of the secondary vegetative part, the length of the secondary shoot, the branching angle between the primary and secondary shoots and the internode length on both order level shoots. This suggested a strong genotypic effect for plant architecture as was previously reported by Kawamura et al., (2011).

Based on our observations, the primary shoots better predict the size of an individual rose plant than do the secondary shoots. Specifically, for a rose plant with a relatively upright shape, the length of the primary shoots better determines its height, while for a rose plant with a prostrate form (or ground cover type), length of primary shoots better determines its width.

Among our populations, the number of flowers also seemed related to the length of pedicels, with the shorter pedicels corresponding to more flowers. This is evident in two of the parental roses: ‘Old Blush’ has the fewest flowers per inflorescence and the longest pedicel among all rose parents, whereas ‘Sweet Chariot’ has the greatest number of flowers per inflorescence and the shortest pedicels.

The strongest correlations found were those for the same traits (the number of nodes and the length) between the vegetative part and shoot on both order level shoots. High correlations were found for the same traits (the number of inflorescence nodes and flower number) between the primary and secondary organs. Moderate to high correlations were found between the number of nodes and the length within the primary and/or secondary order shoots. Moderate correlation was found for the same traits the length of the reproductive part and the internode length between the primary and secondary shoots (Tables 14-17). Kawamura et al., (2011) found correlations for the same traits (internode length, the number of nodes of the inflorescence) between the primary and secondary order shoots, and thus consistent with our results.

The number of flowers on the primary inflorescence was weakly to moderately correlated to multiple traits including the number of nodes on the primary and secondary

vegetative parts, the reproductive parts and shoots, the length of the primary vegetative part, the length of primary, secondary reproductive parts and the shoots (Table 17). Kawamura et al., (2011) noted good correlations with the number of flowers with various inflorescence traits such as the number of nodes (primary and secondary orders), internode length (secondary order), and the number of tertiary shoots formed.

No correlation was seen between the architectural traits concerning branching process (branching angles) and growth processes indicating that it was independent of both vegetative traits and reproductive growth processes (Table 17).

Based on the principal component analysis, the important variables that explained the variability of plant architecture in the preliminary study included: the length of the primary and secondary reproductive parts, the internode length of the secondary shoot, and the number of nodes on the secondary shoot.

2.6 Selection on architectural traits best representing rose plant architecture

The phenotyping work on rose plant architecture involving genetic, environmental and G × E interaction analysis requires measurements on a large number of rose plants. Therefore, as the process is time-consuming and labor-intensive, it was imperative to select fewer traits that were independent (not correlated) with each other.

A selection of architecture traits that are most relevant for characterizing rose plant architecture should meet the following criteria:

- To represent distinct aspects of variables describing plant architecture, i.e., including vegetative traits, reproductive traits, and branching angle;

- To explain the architectural variability observed;
- And to combine correlated variables into one.

The principal component analysis indicated that key traits in explaining the data variation are the following traits: the number of nodes on the secondary shoot, the length of reproductive parts on both primary and secondary shoots, and the internode length of both primary and secondary shoots. The internode length would be equivalent to the trait number of metamers on long axes used by Crespel et al., (2013) and would also reflect the average internode length used by Kawamura et al., (2011).

In addition to these Crespel et al., (2013), Kawamura et al., (2011) and Gitonga et al., (2014) also measured plant form by examining number of determined axes (number of primary shoots, number of side shoots), plant height, stem length, the branching angles (branching angle of the cord in relation to the vertical axis; stem elevation with plant height), and branching order number.

Thus based on our work and that of others, the architectural traits that are important are the length of shoot, the number of nodes on the shoot, branching angles, the number of primary shoots, and traits for characterizing the number of branching orders.

All the analysis above resulted in the new architectural traits evaluated in our subsequent study. They were, plant height (correlated to branching angles), the length of the primary shoot, the number of nodes on the primary shoot, the number of primary shoots, the number of secondary shoots per primary shoot and the number of tertiary shoots per primary shoot.

CHAPTER III

HERITABILITY OF *ROSA* SPP. PLANT ARCHITECTURE IN DIPLOID ROSES

3.1 Synopsis

Six rose plant architectural traits were evaluated for two seasons, May and December of 2015 in College Station, TX to estimate variability and heritability. Seedlings from 13 F_1 families were evaluated. Most traits showed a substantial amount of variability. A random effects model Restricted Maximum Likelihood (REML) analysis indicated that all of the architectural traits demonstrated low to moderate narrow sense heritability (0.12-0.50) and low to high broad sense heritability (0.25-0.92). Traits with low to moderate narrow sense heritability but high broad sense heritability (plant height, number of primary shoots and the length of primary shoots) indicate an important non-additive genetic component. The number of nodes on the primary shoots, the number of secondary and tertiary shoots per primary shoot showed a strong genotype by environment interaction which was a reflection of how the plants grow after the initial spring/early summer flush. Most (11 out of 13) families showed an increased number of secondary/tertiary shoots per node on the primary shoot in December versus May. The comparison of the architectural traits between desirable and undesirable types indicated that the key trait for the selection of a desirable growth type is the number of primary shoots they produce and secondarily the number of secondary and tertiary shoots produced.

3.2 Introduction

3.2.1 Genotype × environment interaction in plant architecture

Plant architecture is the result of growth and branching processes. The components of its variation include genetic, environmental factors and the genotype × environment interaction (Crespel et al., 2014). Plant architecture determines a plant's aesthetic value, which strongly affects its economic value. Architecture is also linked to yield in rose (number of flowers) as well as other crops such as cowpea, (the number of flowers, the number of shoots and pods per plant) (Shimelis and Shiringani, 2010), and in wheat (plant height and spike length) (Wu et al., 2012). Various environmental factors such as temperature (Khayat and Zieslin, 1982; Battey, 2000), the quantity and quality of light (Kawamura and Takeda, 2002; Niinemets and Lukjanova, 2003; Evers et al., 2006; Girault et al., 2008; Rameau et al., 2015), water supply (Cameron et al., 2006; Burnett and van Iersel, 2008; Demotes-Mainard et al., 2013; Huché-Thélier et al., 2013) and mechanical stimulation (Morel et al., 2012) modify architectural traits such as metamer length, the number of shoots and their position along the axis. More research into the heredity of architectural characteristics and the G × E interaction are needed to further understand and manage plant architecture.

3.2.2 Heritability of architectural traits in rose

Quantitative studies on the genetic variability of plant architecture are not easy (Costes et al., 2004; Segura et al., 2006; 2008), because although the plant constructs its

architecture with modular units (leaf, part and shoot) (White, 1979), the architectural traits have variation within a plant (Kawamura, 2010). Additionally, because of the modular nature in plants, the architecture of plants with the same genes may vary due to abiotic (Wu and Stettler, 1997) and biotic (Wei et al., 2013) environmental stresses. These properties of plant architecture cause phenotyping bottlenecks and make it difficult for predicting genetic variances (Furbank and Tester, 2011). Due to their complex plant architecture, it requires much time and space for growth before they are able to be characterized for plant architecture. As a result, the studies on genetics of woody plant architecture are rare compared with model herbaceous plants such as *Arabidopsis thaliana* and rice (*Oryza sativa* L.) (Busov et al., 2008).

Work on rose growth forms has suggested that major genes may be involved in the inheritance of loose arching form in *Rosa caninae (*Wissemann et al., 2006), the dwarf character in diploid roses (Dubois and De Vries, 1987), and the sprawling ground cover versus spreading bush growth type in a tetraploid rose population (Rajapakse et al., 2001).

More recently, Kawamura et al., (2011, 2015) quantified the genetic variability and inheritance of architecture traits in a F_1 diploid rose population, and also conducted QTL mapping studies of inflorescence architecture. Their research reported high broad-sense heritability for inflorescence architectural traits in diploid roses. They identified key genomic regions controlling the traits and proposed that the genes involved in floral initiation are candidate genes controlling the rose inflorescence architecture.

3.2.3 Objectives

The objectives of this study were to evaluate the genetic variation and heritability of six plant architectural traits within 13 diploid rose populations and the desirable levels of architectural traits for an ideal plant for garden use.

3.3 Materials and methods

3.3.1 Plant materials

Diploid rose populations (Table 21) were derived from the hybridization of rose parents with diverse plant architecture. Thirteen F_1 rose populations were used for this study (Figure 15). Based on Peace et al., (2014), we calculated the optimal family size representing the important breeding parents in our germplasm for phenotyping and genotyping QTL of the targeted traits, which is also both financially and logistically feasible to our program. Forty seedlings per family allowed the detection of a QTL of 10-20% effect with 80-90% probability. Thus for the families whose size is larger than 40, we evaluated 40 seedlings per family, and for those smaller than 40, we evaluated all seedlings. Measurements were made on three shoots that grown from base of the plant per seedling for architectural traits.

Table 21. Thirteen diploid rose families evaluated.

FP[1]	MP[2]	Population size (phenotyped number in May & Dec)	Cross year
J06-20-14-3	Sweet Chariot	57 (40, 40)	2010
Sweet Chariot	J06-20-14-3	25 (25, 25)	2012
J06-20-14-3	Little Chief	140 (40, 36)	2011
J06-20-14-3	Red Fairy	130 (40, 39)	2012
J06-20-14-3	Vineyard Song	93 (40, 37)	2010
Vineyard Song	J06-20-14-3	12 (11, 11)	2010
M4-4	Sweet Chariot	27 (27, 23)	2010
Sweet Chariot	M4-4	118 (40, 39)	2010
M4-4	Vineyard Song	10 (5, 5)	2011
Old Blush	J06-30-3-6	112 (40, 36)	2010
Old Blush	M4-4	18 (16, 15)	2010
Old Blush	Red Fairy	158 (40, 40)	2012
J06-30-3-3	Red Fairy	40 (29, 29)	2010

[1] Female parent
[2] Pollen parent

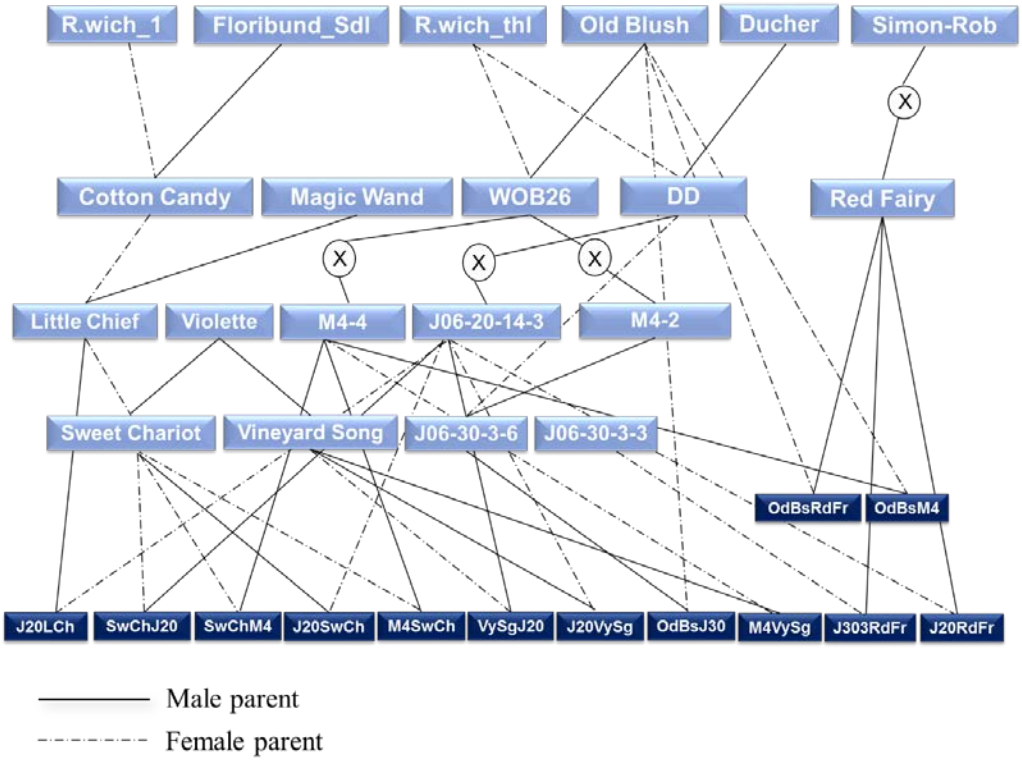


Figure 15. Pedigree diagram of 13 rose populations.

3.3.2 Field experiment and trait assessment

The seedlings of 13 diploid populations in this study were planted at a 1 m × 1 m × 3.5 m spacing in a field two miles from Texas A&M University in College Station. The soil in this field belongs to the Zack-Boonville-Zulch unit (Figure 4 and Soil survey of Brazos County, Texas), which is a dark brown, strongly acid fine sandy loam. The main problem with this type of soil is low fertility, drought, poor drainage due to a clay pan and a severe hazard of erosion. The individual plants were planted in rows oriented east to west in an open field. Raised beds were constructed in the field and black cloth weed barrier was placed around the rose bushes for weed control. The irrigation was applied as needed without the application of fungicides or pesticides during the evaluation. Pruning was conducted in March for removing dead tissue and to synchronize the growth of the seedlings. Each genotype is represented by one plant in the field. The evaluation for plant architecture was done in the field over two seasons in 2015, spring (May) 2015, and winter (December) 2015 (Table 22). The latitude of the location is 30.6504 North and the longitude of it is -96.3226.

Table 22. Monthly temperature and precipitation of 2015 in College Station, TX (National Weather Service, 2015)

	Maximum (°C)	Minimum (°C)	Mean	Total precipitation (mm)
January	13.7	3.5	8.6	169
February	15.8	4.8	10.3	19
March	20.3	10.2	15.3	148
April	26.3	16.6	21.4	122
May	28.7	19.7	24.2	247
June	32.3	22.8	27.6	132
July	35.4	23.4	29.4	36
August	36.2	23.7	29.9	34.5
September	33.4	21.7	27.6	44
October	29.6	17.1	23.3	224
November	21.5	11.6	16.6	128
December	20.1	8.4	13.7	205

3.3.2.1 Measurements of the traits of plant architecture

Six traits best representing distinct aspects of plant architecture were selected based on the preliminary study (Chapter II) and previous studies on rose architecture (Kawamura et al., 2011; Crespel et al., 2013; Gitonga et al., 2014). They were plant height (cm) (Figure 16), the number of primary shoots (Figure 17), the length of the primary shoot (cm) (Figure 18), the number of nodes on the primary shoot (Figure 19), the number of secondary shoots per primary shoot (Figure 20) and the number of tertiary shoots per primary shoot (Figure 21).

Figure 16. Plant height (cm) as measured in the genetic study of plant architecture of 13 diploid rose families.

Figure 17. The number of primary shoots as measured in the genetic study of plant architecture of 13 diploid rose families.

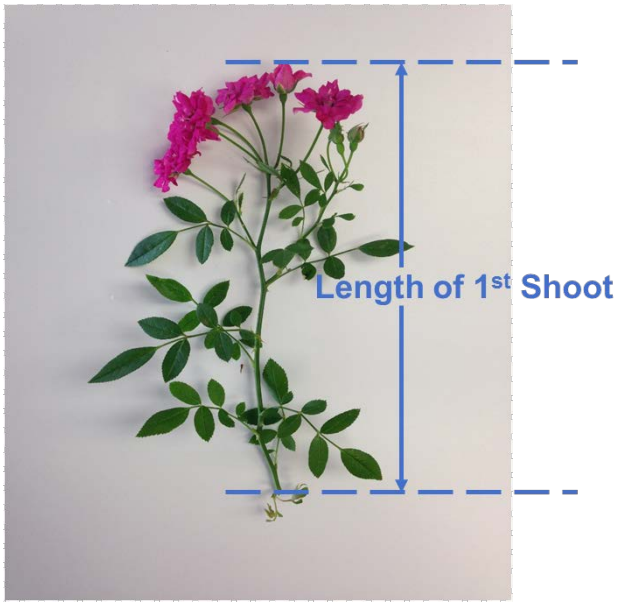


Figure 18. The length of the primary shoots (cm) as measured in the genetic study of plant architecture of 13 diploid rose families.

Figure 19. The number of nodes on the primary shoots as measured in the genetic study of plant architecture of 13 diploid rose families.

Figure 20. The number of secondary shoots per primary shoot as measured in the genetic study of plant architecture of 13 diploid rose families.

Figure 21. The number of tertiary shoots per primary shoot as measured in the genetic study of plant architecture of 13 diploid rose families.

3.3.3 Statistical analysis

The statistical analysis was conducted by using JMP software, Version 12. Frequency distributions of the architectural traits in 13 diploid rose populations were subjected to normality analysis (original and transformed by taking log, log10 and square root) using the Shapiro-Wilk test.

The variance components were calculated with the restricted maximum likelihood (REML) method assuming all factors as random effects for a more powerful estimation (Dieters et al., 1995; Littell, 1996). The model for heritability analysis was: $Y = \mu + Female + Male + Progeny\ (Female, Male) + Season + Season \times Female + Season \times Male + Season \times Progeny\ (Female, Male)$. Because we only have one rose seedling per genotype, residual was confounded with Season × Progeny (Female, Male). The variances of the parents were considered as additive variance (V_A), the progeny variance were considered as non-additive variance (V_D), repeated measurement between May and December data variance was considered as variance of the environment (V_E), the sum of seasonal interactions ($V_{G\times E}$) was also estimated (Connor et al., 2005). Narrow (h^2) and broad sense (H^2), heritability were estimated by the genetic variance from the REML model, where $V_P = (V_A+V_D+V_{G\times E}/E)$, $h^2 = V_A/V_P$, $H^2 = (V_A+V_D)/V_P$ (Hallauer et al., 2010).

Selected desirable and undesirable growth types were subjected to a comparison of means of all six architectural traits among rose families with season to determine key traits for the selection of desirable growth types.

3.4 Results

3.4.1 Distribution of six architectural traits

Based on the normality test, the distribution of plant height and the length of the primary shoot fit a normal distribution. The transformation of data of the other architectural traits did not show substantial improvement of normality. Thus all subsequent statistical analyses were based on the original data.

A substantial amount of variability was associated with plant height (range 17 to 62 cm, mean of 39 cm in May and range 14 to 64 cm, mean of 38 cm in December, Table 23, Figure 22), the number of primary shoots (range 3 to 53, mean of 23 in May, and range 3 to 51, mean of 23 in December, Table 23, Figure 23), the length of the primary shoot (range 17 to 64 cm, mean of 39 cm in May, and range 14 to 62 cm, mean of 37 cm in December, Table 23, Figure 24), the number of nodes on the primary shoot (range 3 to 17, mean of 9.5 in May, and range 4 to 18, mean of 10.4 in December, Table 23, Figure 25). The number of secondary shoots per primary shoot (range 0 to 6, mean of 2.0 in May, and range 0 to 10, mean of 4.5 in December, Table 23, Figure 26), and the number of tertiary shoots per primary shoot (range 0 to 6, mean of 0.7 in May, and range 0 to 15, mean of 4.2 in December, Table 23, Figure 27) were skewed towards zero. The traits that exhibited substantial variability should allow for genetic improvement.

There were differences among the populations in all of the architectural traits measured as well as differences among the data taken in the early (May) versus the late (December) season in the number of nodes on the primary shoot, the number of

secondary shoots per primary shoot and the number of tertiary shoots per primary shoot. Although plant height, the number of primary shoots, and the length of the primary shoot were predictable with early season information, the growth of the number of nodes for primary/secondary/tertiary varied among the populations during the season (Tables 23-27).

Table 23. Comparison of seasonal means and range of architectural traits for 13 rose families evaluated in the field in May and December of 2015, in College Station, TX.

	May		Dec		Sig.
	Mean	**Range**	**Mean**	**Range**	
Plant height (cm)	39	(17-62)	38	(14-64)	NS
Number of primary shoots	23	(3-53)	23	(3-51)	NS
Length of 1st shoot (cm)	39	(17-64)	37	(14-62)	NS
Number of nodes on 1st shoot	9.5	(3-17)	10.4	(4-18)	***
Number of 2nd shoots per 1st shoot	2.0	(0-6)	4.5	(0-10)	***
Number of 3rd shoots per 1st shoot	0.7	(0-6)	4.2	(0-15)	***

NS, *, **, *** Non-significant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively

Table 24. Analysis of variance for six architectural traits in 13 diploid rose families evaluated in the field in May and December of 2015, in College Station, TX.

	Family	Season	Family × Season
Plant height (cm)	***	NS	NS
Number of primary shoots	***	NS	NS
Length of 1st shoot (cm)	***	NS	*
Number of nodes on 1st shoot	***	***	***
Number of 2nd shoots per 1st shoot	***	***	***
Number of 3rd shoots per 1st shoot	***	***	***

NS, *, **, *** Non-significant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively

Table 25. Mean separations of six architectural traits for 13 rose families evaluated in the field in May and December of 2015, in College Station, TX.

	Plant height (cm)	**#1st shoots**	**Length of 1st shoots (cm)**	**#Nodes on 1st shoot**	**#2nd shoots per 1st shoot**	**#3rd shoots per 1st shoot**
J06-20-14-3 × Little Chief	27 f	18 e	32 fg	12.0 ab	4.3 ab	4.1 a
J06-20-14-3 × Red Fairy	37 d	22 d	42 bc	10.9 bc	3.9 bc	3.0 bc
J06-20-14-3 × Sweet Chariot	39 cd	27 ab	35 ef	9.1 e	3.0 df	1.7 de
J06-20-14-3 × Vineyard Song	38 cd	24 bd	43 bc	11.4 bc	2.7 ef	1.0 e
J06-30-3-3 × Red Fairy	39 bd	21 de	39 cd	9.6 de	3.9 bc	3.5 ac
M4-4 × Sweet Chariot	32 e	23 bd	36 df	9.4 de	3.3 ce	2.2 ce
M4-4 × Vineyard Song	38 be	31 ac	54 a	14.1 a	5.8 a	3.7 ae
Old Blush × J06-30-3-3	39 bd	23 bd	39 ce	8.4 ef	2.4 f	1.6 de
Old Blush × M4-4	36 de	25 bd	29 g	6.7 f	2.7 df	3.1 ad
Old Blush × Red Fairy	45 a	13 f	39 cd	9.2 e	2.9 ef	1.6 de
Sweet Chariot × J06-20-14-3	37 d	23 cd	43 bc	12.9 a	4.4 ab	3.8 ab
Sweet Chariot × M4-4	41 bc	26 bc	39 cd	10.5 cd	3.8 bd	3.2 ac
Vineyard Song × J06-20-14-3	45 ab	33 a	48 ab	12.6 ac	2.5 cf	1.1 ce
n	272	272	272	272	272	272

Levels not connected by same letter are significantly different and the mean separation is within a column.

Table 26. Two-way ANOVA comparing means of the length of primary shoot and the number of nodes on the primary shoot for 13 rose families characterized in May and December of 2015, in College Station, TX.

	Length of 1st Shoot (cm)			#Nodes on 1st Shoot		
	May	**Dec**	**Sig.**	**May**	**Dec**	**Sig.**
J06-20-14-3 × Little Chief	36	29	NS	11.7	12.3	NS
J06-20-14-3 × Red Fairy	44	41	NS	10.7	11.1	NS
J06-20-14-3 × Sweet Chariot	37	34	NS	9.6	8.6	NS
J06-20-14-3 × Vineyard Song	40	46	*	9.5	13.2	***
J06-30-3-3 × Red Fairy	41	37	NS	9.5	9.6	NS
M4-4 × Sweet Chariot	36	36	NS	8.6	10.1	NS
M4-4 × Vineyard Song	47	57	*	12.0	16.3	*
Old Blush × J06-30-3-3	40	38	NS	7.7	9.1	NS
Old Blush × M4-4	27	30	NS	6.1	7.3	NS
Old Blush × Red Fairy	40	39	NS	9.1	9.2	NS
Sweet Chariot × J06-20-14-3	44	41	NS	13.7	12.0	NS
Sweet Chariot × M4-4	42	37	NS	10.0	11.0	NS
Vineyard Song × J06-20-14-3	44	52	NS	9.0	16.3	***
n		272			272	

NS, *, **, *** Non-significant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively

Table 27. Two-way ANOVA comparing means of the number of secondary shoots per primary shoot and the number of tertiary shoots per primary shoot for 13 rose families characterized in May and December of 2015, in College Station, TX.

	#2nd shoots per 1st shoot			#3rd shoots per 1st shoot		
	May	**Dec**	**Sig.**	**May**	**Dec**	**Sig.**
J06-20-14-3 × Little Chief	3.3	5.3	***	2.0	6.3	***
J06-20-14-3 × Red Fairy	3.0	4.7	***	1.2	4.8	***
J06-20-14-3 × Sweet Chariot	2.2	3.8	***	0.7	2.7	**
J06-20-14-3 × Vineyard Song	0.8	4.6	***	0.1	1.9	*
J06-30-3-3 × Red Fairy	2.9	4.9	***	1.4	5.7	***
M4-4 × Sweet Chariot	1.9	4.7	***	0.6	3.8	***
M4-4 × Vineyard Song	2.0	7.7	***	1.3	6.0	*
Old Blush × J06-30-3-3	1.1	3.7	***	0.1	3.1	***
Old Blush × M4-4	0.7	4.8	***	0.2	5.9	***
Old Blush × Red Fairy	1.7	4.0	***	0.3	3.0	***
Sweet Chariot × J06-20-14-3	4.4	4.4	NS	2.3	5.3	***
Sweet Chariot × M4-4	2.6	5.0	***	1.1	5.4	***
Vineyard Song × J06-20-14-3	2.0	3.0	NS	0.5	1.8	NS
n		272			272	

NS, *, **, *** Non-significant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively

Figure 22. Distribution of plant height measured in May (upper) and December (lower), 2015 in College Station, Texas of for 13 rose families x_5 = 39 cm, SD_5 = 8.80 and n_5= 385; x_{12} = 38 cm, SD_{12} = 9.52 and n_{12} = 375 (10 seedlings died).

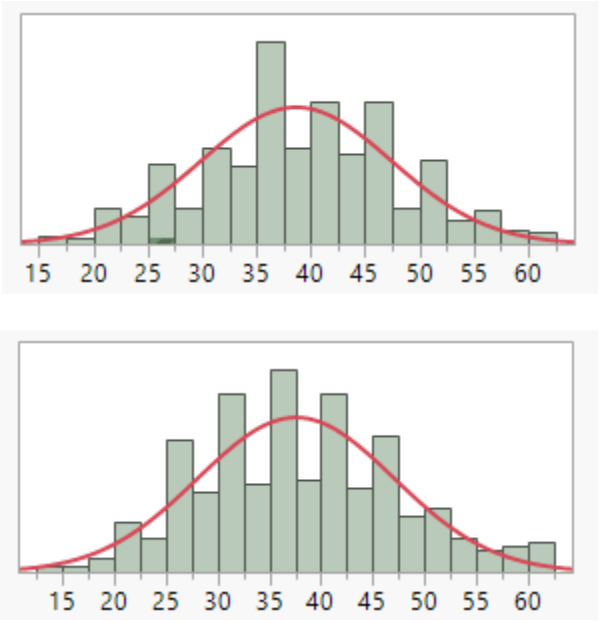


Figure 23. Distribution of the number of the primary shoots measured in May (upper) and December (lower), 2015 in college Station, Texas of for 13 rose families x_5 = 23, SD_5 = 11.02 and n_5 = 385; x_{12} = 23, SD_{12} = 10.69 and n_{12} = 375 (10 seedlings died).

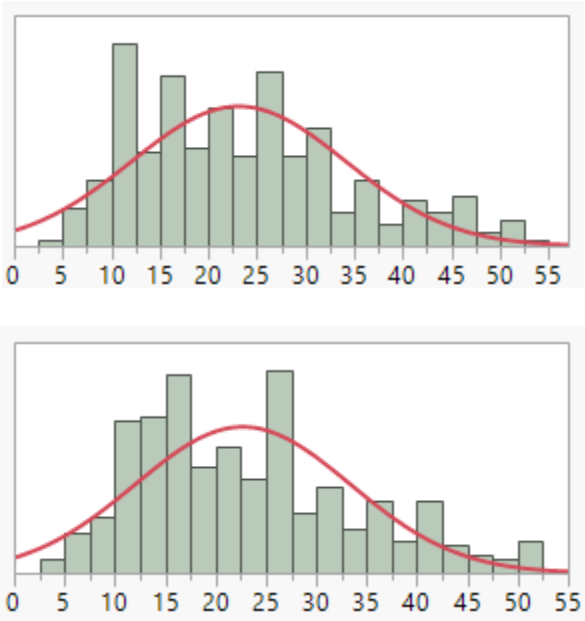


Figure 24. Distribution of the length of the primary shoots (cm) measured in May (upper) and December (lower), 2015 in College Station, Texas of for 13 rose families x_5 = 39 cm, SD_5 = 9.05 and n_5 = 385; x_{12} = 37 cm, SD_{12} = 9.18 and n_{12} = 272.

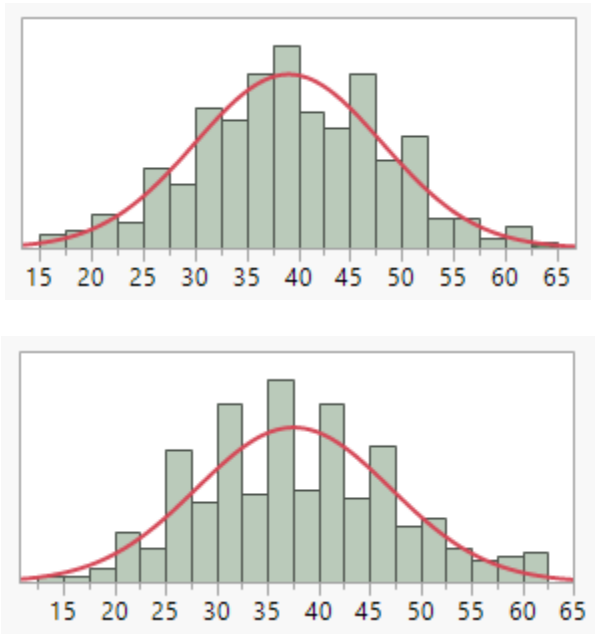


Figure 25. Distribution of the number of nodes on the primary shoot measured in May (upper) and December (lower), 2015 in College Station, Texas of for 13 rose families x_5 = 9, SD_5 = 2.86 and n_5 = 385; x_{12} = 10, SD_{12} = 2.92 and n_{12} = 272.

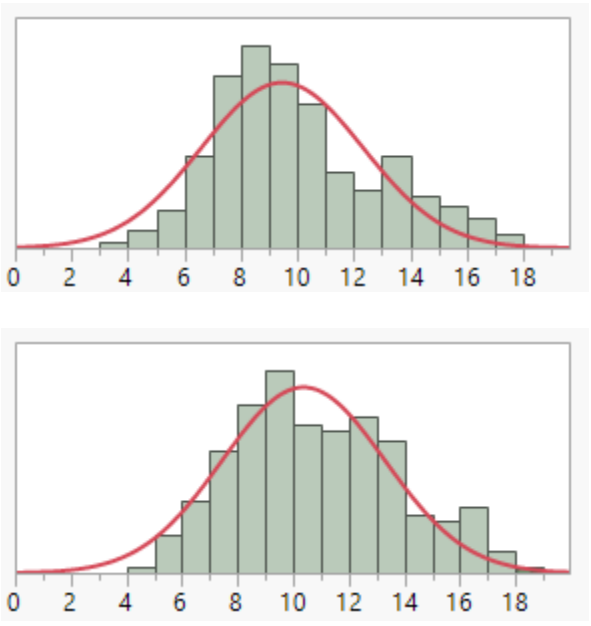


Figure 26. Distribution of the number of secondary shoots per primary shoot measured in May (upper) and December (lower), 2015 in College Station, Texas of for 13 rose families $x_5 = 2$, $SD_5 = 1.56$ and $n_5 = 385$; $x_{12} = 5$, $SD_{12} = 2.05$ and $n_{12} = 272$.

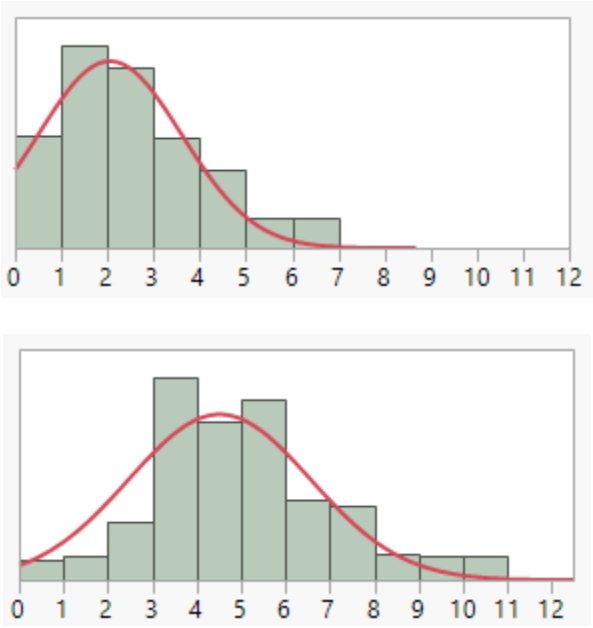
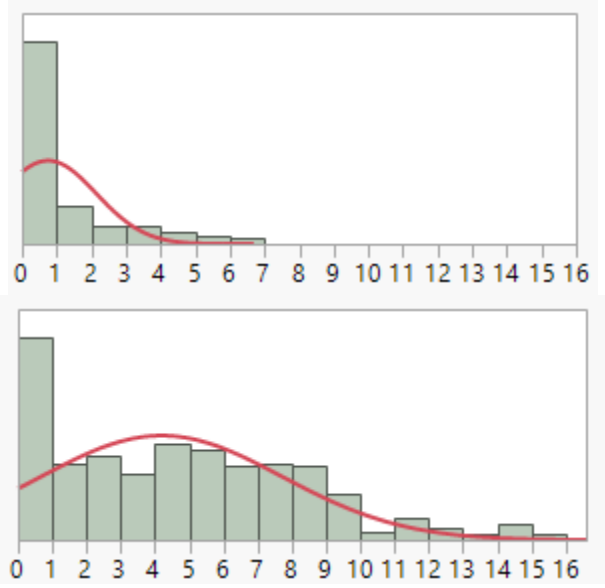


Figure 27. Distribution of the number of tertiary shoots per primary shoot measured in May (upper) and December (lower), 2015 in College Station, Texas of for 13 rose families $x_5 = 1$, $SD_5 = 1.39$ and $n_5 = 385$; $x_{12} = 4$, $SD_{12} = 3.52$ and $n_{12} = 272$.



3.4.2 Heritability analysis: field study of 13 rose families in May and December of 2015

As various rose families differ dramatically in the length and the number of nodes on their shoots, the data for the number of secondary shoots and the number of tertiary shoots were expressed on a per node on the primary shoot basis to standardize the data.

The six architectural traits measured exhibited low to high broad sense heritability (0.25-0.92) and low to moderate narrow sense heritability (0.12-0.50) (Table 28), which indicated that architectural traits are feasible targets of rose breeding.

Plant height measured at the plant level, was found highly heritable with a moderate narrow sense heritability ($h^2 = 0.50$) and high broad sense heritability ($H^2 = 0.82$), which was consistent with estimates previously reported by Gitonga et al., (2014) ($H^2 = 0.82$) and a little lower than that by Kawamura et al., (2015) ($H^2 = 0.88$) (Table 28).

The number of primary shoots had a low narrow sense heritability ($h^2 = 0.27$) and high broad sense heritability ($H^2 = 0.92$), indicating a strong non-additive genetic component which accounted for approximately 60% of total phenotypic variance and was more than twice that of the narrow sense estimate for this trait (Table 28). Previous studies evaluated the number of long axes (shoots have five or more metamers: an internode, a node, an axillary bud and a leaf) and the number of determined axes (axes terminated in a flower bud or a flower) (Crespel et al., 2013; 2014), which are equivalent to some extent to the traits of the number of primary shoots in our study. The broad sense heritability for the number of long axes and the number of determined axes

reported by Crespel et al., (2014) were 0.70 and 0.64 respectively, and thus were lower than that of the number of primary shoots ($H^2 = 0.92$) (Table 28) in our study.

The length of the primary shoot showed low additive variation ($h^2 = 0.20$) and high broad sense heritability ($H^2 = 0.64$) (Table 28). This is higher than a previous report by Crespel et al., (2014) on the length of the long axes ($H^2 = 0.48$). Non-additive genetic variance component accounted for approximately 32% of phenotypic variance compared to 15% (Table 28) for the additive genetic component. The number of nodes on the primary shoot revealed low narrow sense heritability ($h^2 = 0.12$) and moderate broad sense heritability ($H^2 = 0.46$) (Table 28). A previous study reported the broad sense heritability of the number of metamers (an internode, a node, an axillary bud and a leaf) of the long axes which should be a good estimator of the number of nodes on primary shoots in our study. According to Crespel et al., (2014), the broad sense heritability of the number of metamers is 0.95 which is higher than that found in our study on the number of nodes on a primary shoot ($H^2 = 0.46$) (Table 28).

The number of secondary shoots per primary node had low narrow sense heritability ($h^2 = 0.17$) and broad sense heritability ($H^2 = 0.25$) (Table 28). As for the number of tertiary shoots per primary node, narrow sense heritability is low ($h^2 = 0.16$) while broad sense heritability is moderate ($H^2 = 0.40$) (Table 28).

Table 28. Variance component, broad sense heritability (H^2), and narrow sense heritability (h^2) for six plant architectural traits evaluated in the field in May and December of 2015, in College Station, TX.

Traits	N	R^2	Variances					h^2	H^2
			V_A	V_D	V_G	$V_{G\times E}$	V_P		
Plant height (cm)	750	0.70	56.4	36.9	93.3	40.1	113.4	0.50	0.82
Number of 1st shoot	750	0.90	35.8	85.2	121.0	22.1	132.1	0.27	0.92
Length of 1st shoot (cm)	544	0.68	17.9	38.7	56.6	62.4	87.9	0.20	0.64
Number of nodes on 1st shoot	544	0.61	1.2	3.2	4.4	10.1	9.5	0.12	0.46
Number of 2nd shoots per 1st node	544	0.46	0.0033	0.0014	0.0047	0.028	0.019	0.17	0.25
Number of 3rd shoots per 1st node	544	0.48	0.011	0.017	0.028	0.083	0.055	0.16	0.40

N: number of observations; V_A = additive genetic variance; V_D = non-additive genetic variance; V_G = genetic variance (additive and non-additive); V_E = environmental variance; $V_{G\times E}$ = genotype × environmental variance; V_P = phenotypic variance; $V_P = (V_A+V_D+ V_{G\times E}/E)$; $h^2 = V_A/V_P$, $H^2 = (V_A+V_D)/V_P$.

3.4.3 Genotype by environment interaction

Among six architectural traits, plant height and the number of primary shoots showed weak genotype by environment interaction as indicated by the low $V_{G\times E}$ to V_G ratios (0.43 and 0.18, respectively) (Table 29), reflecting genotypic consistency across seasons. The length of the primary shoot was moderately affected by genotype by environment interaction ($V_{G\times E}/V_G$ ratios of 1.10, respectively) (Table 29). A strong genotype by environment interaction was found for the number of nodes on the primary shoot, the number of secondary shoots and tertiary shoots per primary node ($V_{G\times E}/V_G$ ratios of 2.30, 5.96 and 2.96, respectively) which was a reflection of how the plant grows after the initial spring/early summer flush (Table 29). Genotype by environment interaction has been described as differential response of genotypes to the environment in which they are grown (Bernardo, 2010). If such interactions exist in the case of specific genotypes across specific environments, selection on the basis of performance for a given trait cannot be practiced in one environment if the plant is expected to perform the same in another (Allard et al., 1964).

Table 29. Genotypic variance, variance for genotype × environment interaction and ratio of variance of the genotype × environment interaction to the total genetic variance for six plant architectural traits evaluated in the field in May and December of 2015, in College Station, TX.

Traits	N	Variances		
		V_G	$V_{G\times E}$	$V_{G\times E}/V_G$
Plant height (cm)	750	93.3	40.1	0.43
Number of 1st shoot	750	121.0	22.1	0.18
Length of 1st shoot (cm)	544	56.6	62.4	1.10
Number of nodes on 1st shoot	544	4.4	10.1	2.30
Number of 2nd shoots per 1st node	544	0.0047	0.028	5.96
Number of 3rd shoots per 1st node	544	0.028	0.083	2.96

N: number of observations; V_G = genetic variance (additive and non-additive); V_E = environmental variance; $V_{G\times E}$ = genotype × environmental variance.

3.4.4 Two-way ANOVA comparing family, season and family by season means

For the architectural traits subjected to two-way ANOVA comparing family, season and family by season means, most (11 out of 13) families showed an increased number of secondary/tertiary shoots per node on the primary shoot (Table 30). Among those with increased number of secondary and tertiary shoots, the number seen in December at the end of the season varies among populations as well. The 'Old Blush × M4-4' family had the highest (0.64/0.78 secondary/tertiary shoots per primary shoot node) and the 'Vineyard Song × J06-20-14-3' family had the lowest (0.30/0.15

secondary/tertiary shoots per primary shoot node) number of second and third level shoots forming (Table 31).

Table 30. Two-way ANOVA comparing means of the number of secondary shoots per primary node and the number of tertiary shoots per primary node for 13 rose families characterized in May and December of 2015, in College Station, TX.

	#2nd shoots per 1st node			#3rd shoots per 1st node		
	May	**Dec**	**Sig.**	**May**	**Dec**	**Sig.**
J06-20-14-3 × Little Chief	0.28	0.45	***	0.18	0.54	***
J06-20-14-3 × Red Fairy	0.29	0.43	***	0.11	0.46	***
J06-20-14-3 × Sweet Chariot	0.22	0.45	***	0.06	0.29	***
J06-20-14-3 × Vineyard Song	0.08	0.36	***	0.01	0.17	*
J06-30-3-3 × Red Fairy	0.35	0.52	***	0.19	0.62	***
M4-4 × Sweet Chariot	0.23	0.49	***	0.06	0.41	***
M4-4 × Vineyard Song	0.19	0.59	***	0.19	0.35	NS
Old Blush × J06-30-3-3	0.13	0.41	***	0.00	0.38	***
Old Blush × M4-4	0.11	0.64	***	0.03	0.78	***
Old Blush × Red Fairy	0.18	0.44	***	0.03	0.32	***
Sweet Chariot × J06-20-14-3	0.33	0.37	NS	0.17	0.44	***
Sweet Chariot × M4-4	0.25	0.47	***	0.11	0.51	***
Vineyard Song × J06-20-14-3	0.26	0.30	NS	0.05	0.15	NS
n		272			272	

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

Table 31. Mean separations among families of the number of secondary shoots per primary node and the number of tertiary shoots per primary node for 13 rose families characterized in May and December of 2015, in College Station, TX

	#2nd shoots per 1st node		#3rd shoots per 1st node	
	May	**Dec**	**May**	**Dec**
J06-20-14-3 × Little Chief	0.28 ad	0.45 bf	0.18 a	0.54 ac
J06-20-14-3 × Red Fairy	0.29 ac	0.43 bf	0.11 ab	0.46 be
J06-20-14-3 × Sweet Chariot	0.22 de	0.45 bf	0.06 bd	0.29 ef
J06-20-14-3 × Vineyard Song	0.08 g	0.36 e	0.01 d	0.17 f
J06-30-3-3 × Red Fairy	0.35 a	0.52 ab	0.19 a	0.62 ab
M4-4 × Sweet Chariot	0.23 ce	0.49 bf	0.06 bd	0.41 be
M4-4 × Vineyard Song	0.19 bg	0.59 ac	0.19 a	0.35 af
Old Blush × J06-30-3-3	0.13 fg	0.41 cf	0.00 d	0.38 cf
Old Blush × M4-4	0.11 fg	0.64 a	0.03 cd	0.78 a
Old Blush × Red Fairy	0.18 ef	0.44 bf	0.03 cd	0.32 df
Sweet Chariot × J06-20-14-3	0.33 ab	0.37 de	0.17 a	0.44 be
Sweet Chariot × M4-4	0.25 cd	0.47 bf	0.11 ab	0.51 bd
Vineyard Song × J06-20-14-3	0.26 ae	0.30 df	0.05 ad	0.15 df
n	272		272	

Levels not connected by same letter are significantly different and the mean separation is within a column.

3.4.5 Definition of desirable growth type

An assessment of desirable and undesirable combinations of horticultural traits was carried out. We hypothesized that the plant architecture of a desirable plant is different from that of an undesirable one. Generally, rose plants that grow to waist to shoulder height (Waliczek et al., 2015), with relatively compact shape and evenly-distributed flowers are considered as desirable (Figure 30a-d) (Boumaza et al., 2009). For instance, a desirable plant has well-distributed flowers (Figure 28a, b) while the undesirable one has perimeter flowers (Figure 29a, b).

Rose seedlings with an empty center, due to nodes that do not produce shoots or leaves on the lower part of vegetative shoots (see Figure 31a), long flower shoots (Figure 31b-d), and a non-compact and open shape (Figure 31c, d) are considered as undesirable. The value of six architectural traits measured on some of the rose seedlings with desirable and undesirable (Table 32) growth types were examined.

The comparison of the architectural traits between desirable and undesirable types (Table 33) indicated that both types differ little in plant height, shoot length or the number of nodes per shoot. The key trait that differentiates these groups were the number of primary shoots they produced and secondarily the number of secondary and tertiary shoots produced. These are the traits that determine the fullness of the plant which is an important factor affecting its aesthetic value. A rose plant with many primary shoots looks full. However, fewer primary shoots can be compensated by more side shoots to attain a good level of fullness. A desirable growth type has more than thirty primary shoots frequently combined with multiple secondary and tertiary shoots.

Figure 28a & b. Desirable growth type with evenly-distributed flowers.

Figure 29a & b. Undesirable growth type with perimeter flowers.

Figure 30a-d. Rose seedlings with desirable growth type.

Figure 31a-d. Rose seedlings with undesirable growth type.

Table 32. The architectural traits of rose seedlings selected with desirable and undesirable growth types.

Rose seedlings with desirable growth types selected (family)	**Plant height (cm)**	**#1st shoots**	**Length of 1st shoot (cm)**	**#Nodes on 1st shoot**	**#2nd shoots per 1st shoot**	**#3rd shoots per 1st shoot**
11112-N005 (M4-4 × Vineyard Song)	45	52	34	6	1	0
10071-N010 (Vineyard Song × J06-20-14-3)	58	36	40	12	5	7
10074-P35 (J06-20-14-3 × Sweet Chariot)	36	51	37	9	3	0
10074-N078 (J06-20-14-3 × Sweet Chariot)	56	50	48	8	5	5
10043-N049 (Sweet Chariot × M4-4)	60	42	32	7	5	6
Rose seedlings with undesirable growth types selected (family)	**Plant height (cm)**	**#1st shoots**	**Length of 1st shoot (cm)**	**#Nodes on 1st shoot**	**#2nd shoots per 1st shoot**	**#3rd shoots per 1st shoot**
10074-N011(J06-20-14-3 × Sweet Chariot)	45	10	35	6	1	0
10038-N100 (Old Blush × J06-30-3-6)	38	6	43	7	2	0
10071-N006 (Vineyard Song × J06-20-14-3)	38	23	61	13	0	0
12062-N001 (Old Blush × Red Fairy)	62	16	62	12	4	0
10075-N013 (M4-4 × Sweet Chariot)	18	10	26	6	1	0

Table 33. Compare means of six architectural traits between desirable and undesirable growth types.

	Desirable	Undesirable	Significance
Plant height (cm)	51.0	40.2	NS
#1st shoots	46.2	13.0	***
Length of 1st shoot (cm)	38.2	45.4	NS
#Nodes on 1st shoot	8.4	8.8	NS
2nd shoots per 1st shoot	3.8	1.6	*
3rd shoots per 1st shoot	3.6	0	*

NS, *, **, *** Non-significant or significant at $P \leq 0.05$, 0.01, or 0.001, respectively

3.5 Discussions and conclusions

Most architectural traits evaluated in our study were associated with high phenotypic variability, while the number of secondary and tertiary shoots were skewed to zero. Variability is a major component in the estimation of heritability, and both are necessary for genetic improvement.

The six architectural traits measured exhibited low to high broad sense heritability (0.25-0.92) and low to moderate narrow sense heritability (0.12-0.50). Broad-sense heritability (H^2) has been used as an index of reliability of phenotypic selection for genetic characters (Holland et al., 2003), and the accuracy of QTL analysis depends largely on the level of H^2 (Beavis, 1998). As the rose is a vegetatively propagated crop, the non-additive genetic component of the variation can be captured easily by clonal propagation. Our results combined with previous studies (Kawamura et al., 2015; Crespel et al., 2014) that reported

high broad sense heritability for several architectural traits of garden roses, indicated that rose plant architecture is a feasible target for rose breeding. Architectural traits with low narrow sense heritability but moderately high to high broad sense heritability such as the number of primary shoots, the length of the primary shoot and the number of nodes on the primary shoot in our study suggested important non-additive effects.

Architectural traits were affected by genotype by environment effect to different extents. Plant height and the number of primary shoots were highly heritable and consistent over seasons, and thus can be reliably and accurately measured and selected in any season of the year. While the number of secondary shoots and tertiary shoots per primary showed lower heritabilities and tended to increase in number as the season progressed. The extent of this side shoot growth varied by population (high G × E interaction). This would indicate that selection in the early season would not predict the final number of secondary/tertiary shoots forming throughout the year. Therefore, selection in both the early and late season is recommended.

Pruning is an economical and practical technique for plant growth control (Hassanein, 2010). Younis et al., (2013) studied on the effect of different pruning times during the winter months on the growth of *Rosa centifolia* and concluded that pruning during early winter increases the plant height, the number of shoots and other vegetative characteristics of rose plants. The study of Saffari et al., (2004) revealed that the pruning time at first week of March had the most significant effect on the increase of plant height. Therefore, further studies on the timing and type of pruning to improve rose plant architecture are recommended.

The comparison of the architectural components between desirable and undesirable types indicated that the key traits for the selection of a desirable growth type are the number of primary shoots and the number of secondary and tertiary shoots produced. Of these traits, the number of primary shoots will be the easiest to improve as it has a moderately low narrow sense heritability but a high broad sense heritability indicating strong non-additive genetic effects. The other two traits, have low narrow sense heritability and low to moderate broad sense heritabilities indicating a more difficult path to increasing their numbers by selection.

Future studies could focus more on the development of inflorescence components. Our ultimate goal is to select rose plants that not only have desirable growth types, but also bloom consistently throughout the year. The next step would be to track the flowering behavior of the plant throughout the year. This would include the development of shoots and the pattern of flower opening among the various levels of inflorescences as they develop and relate it to the flower intensity and flower distribution on the plant throughout the growing season. As we do these field studies on a range of roses (cultivars, desirable and undesirable growth types) and rose populations, the temperature data needs to be recorded to assess the effect of temperature on rose growth and flower production.

CHAPTER IV

SUMMARY

In the preliminary study, we characterized rose plant architecture on the basis of its growth (vegetative and reproductive) and branching processes. Most architectural components differed among four rose families, suggesting a strong genotypic effect for plant architecture. The strongest correlations found were those for the same traits (the number of nodes and the length) between the vegetative part and shoot on both order level shoots. High correlations were found for the same traits (the number of inflorescence nodes and flower number) between the primary and secondary organs. Moderate to high correlations were found between the number of nodes and the length within the primary and/or secondary order shoots. Moderate correlation was found for the same traits the length of the reproductive part and the internode length between the primary and secondary shoots. No correlation was seen between the architectural traits concerning branching process (branching angles) and growth processes indicating that it was independent of both vegetative traits and reproductive growth processes.

Most architectural traits evaluated in our major study were associated with high phenotypic variability, while the number of secondary and tertiary shoots were skewed to zero. The six architectural traits measured exhibited low to high broad sense heritability and low to moderate narrow sense heritability. Additionally, architectural traits were affected by genotype by environment effect to different extents. Plant height and the number of primary shoots were highly heritable and consistent over seasons, while the number of secondary shoots and tertiary shoots per primary showed lower heritabilities and tended to increase in number as the season progressed. The comparison of the architectural components between

desirable and undesirable types indicated that the key traits for the selection of a desirable growth type are the number of primary shoots and the number of secondary and tertiary shoots produced.

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APPENDIX A

SCATTER PLOTS FOR HIGHLY AND MODERATELY CORRELATED TRAITS
($R \geq 0.65$ AND $0.64 \geq R \geq 0.50$)

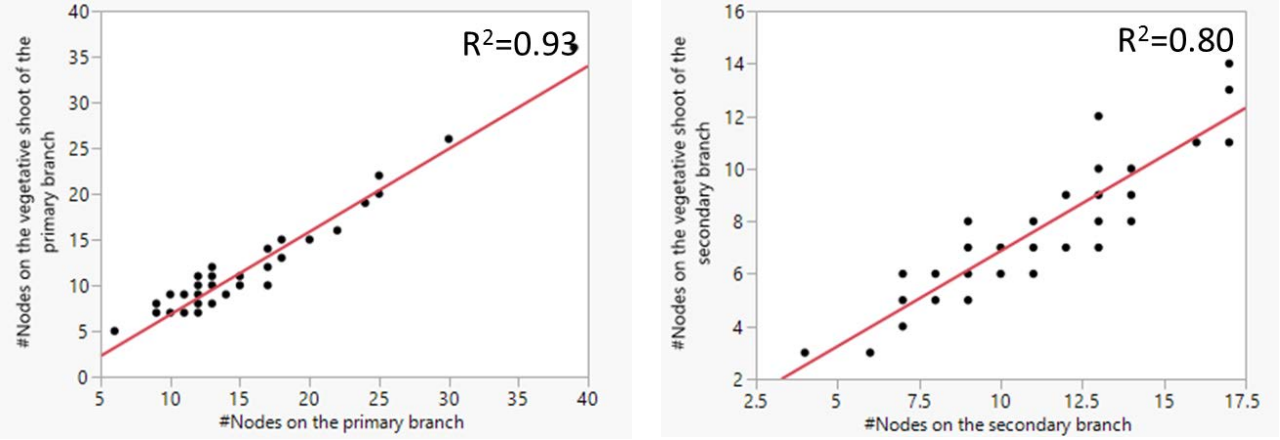

Figure A1. Left: scatter plot of correlation between the number of nodes on the primary shoot and the number of nodes on the vegetative part of the primary shoot. Right: scatter plot of correlation between the number of nodes on the secondary shoot and the number of nodes on the vegetative part of the secondary shoot.

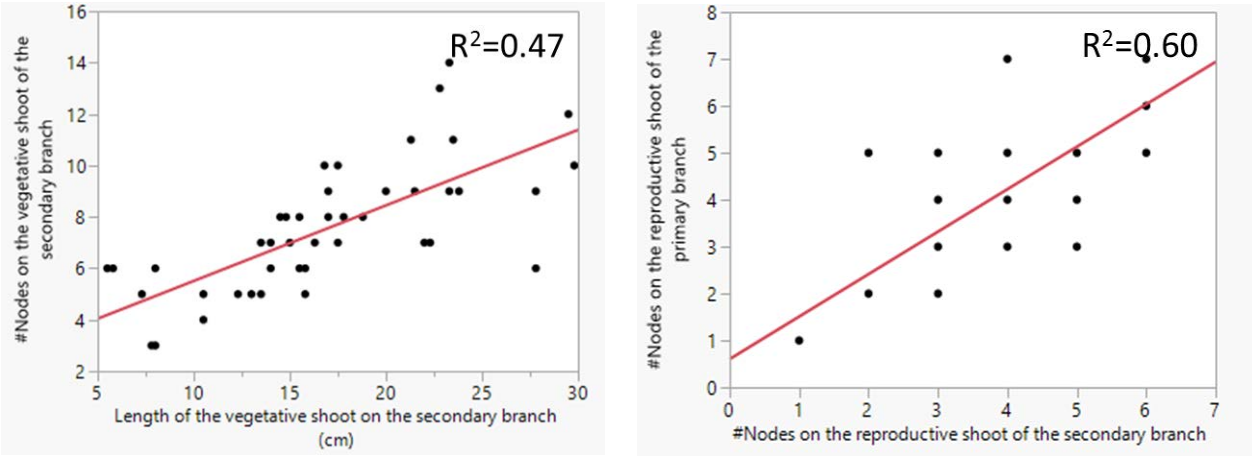

Figure A2. Left: scatter plot of correlation between the length of the vegetative part on the secondary shoot and the number of nodes on the vegetative part of the secondary shoot. Right: scatter plot of correlation between the number of nodes on the reproductive part of the secondary shoot and the number of nodes on the reproductive part of the primary shoot.

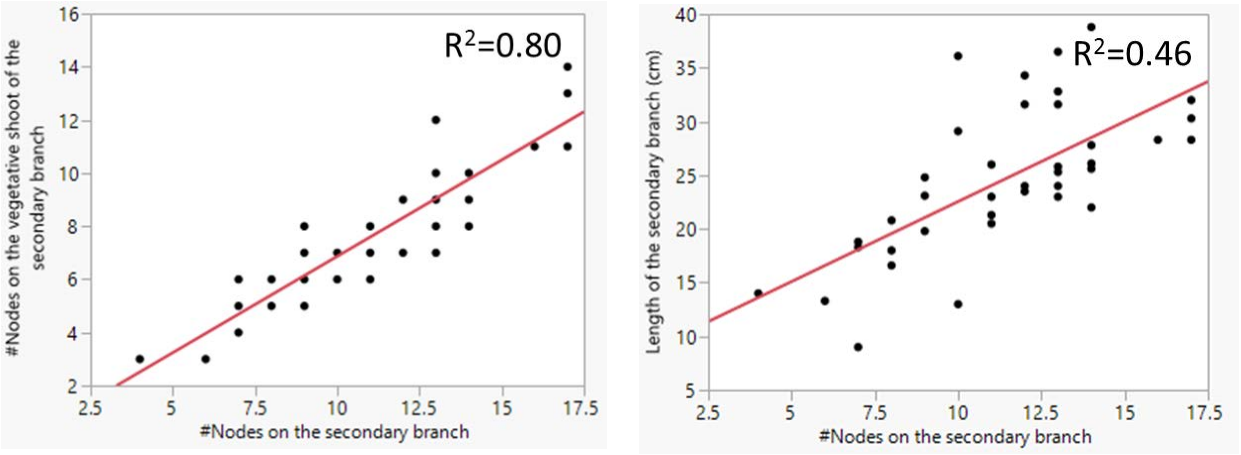

Figure A3. Left: scatter plot of correlation between the number of nodes on the secondary shoot and the length of the vegetative part of the secondary shoot. Right: scatter plot of correlation between the number of nodes on the secondary shoot and the length of the secondary shoot.

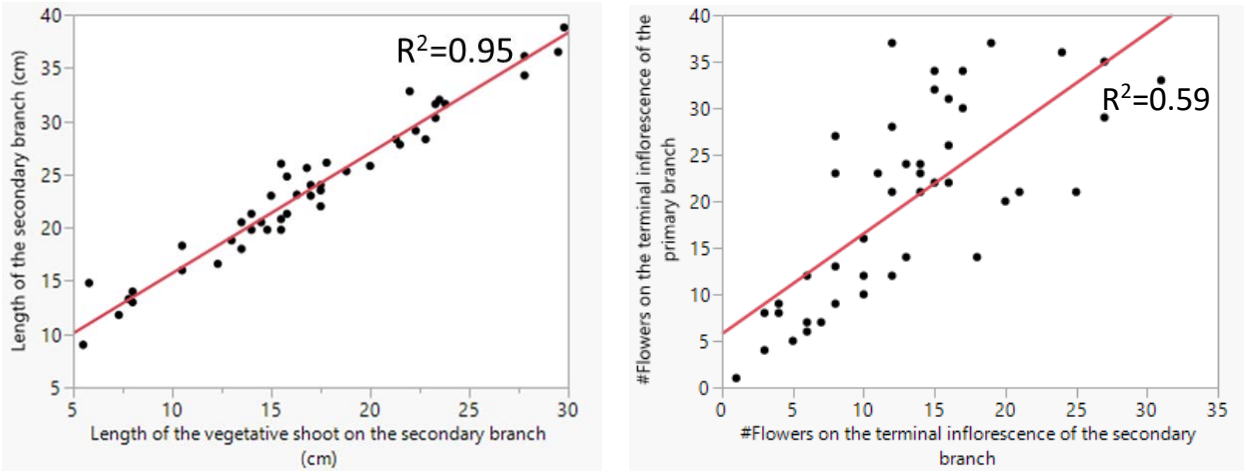

Figure A4. Left: scatter plot of correlation between the length of the vegetative part on the secondary shoot and the length of the secondary shoot. Right: scatter plot of correlation between the number of flowers on the terminal inflorescence of the secondary shoot and the number of flowers on the terminal inflorescence of the primary shoot.

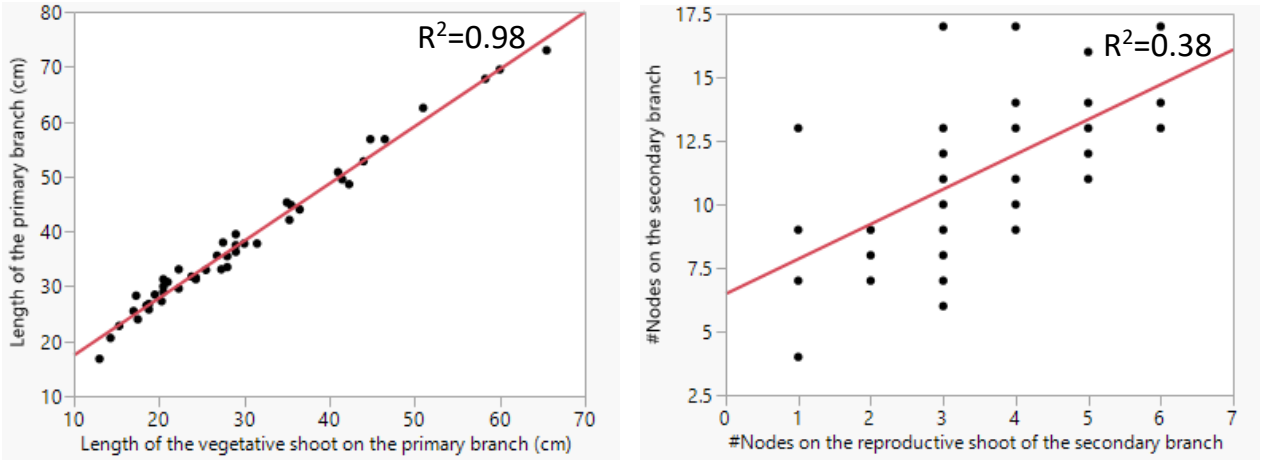

Figure A5. Left: Scatter plot of correlation between the length of the vegetative part on the primary shoot and the length of the primary shoot. Right: scatter plot of correlation between the number of nodes on the reproductive part of the secondary shoot and the number of nodes on the secondary shoot.

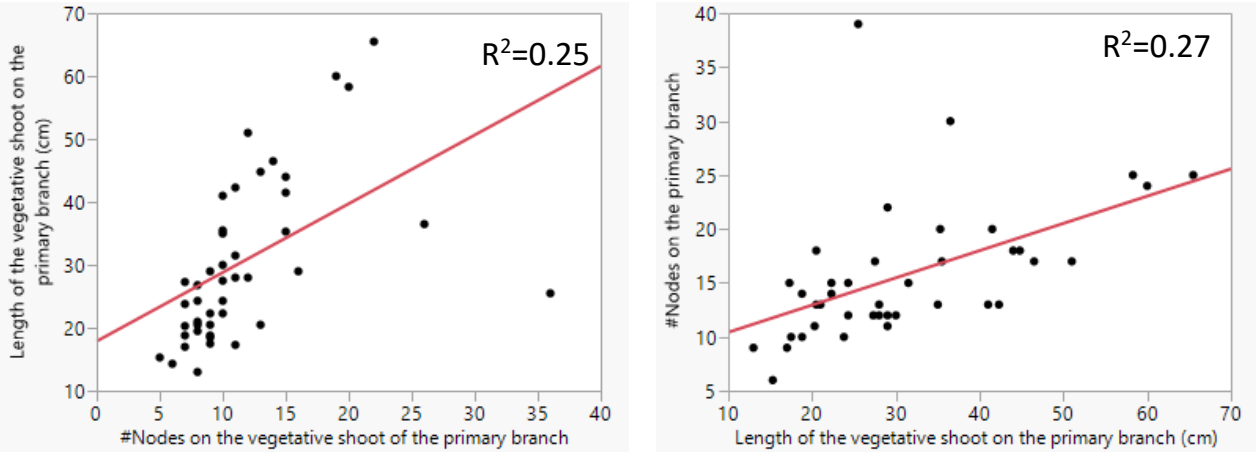

Figure A6. Left: scatter plot of correlation between the length of the vegetative part on the primary shoot and the length of the primary shoot. Right: scatter plot of correlation between the length of the vegetative part of the primary shoot and the number of nodes on the primary shoot.

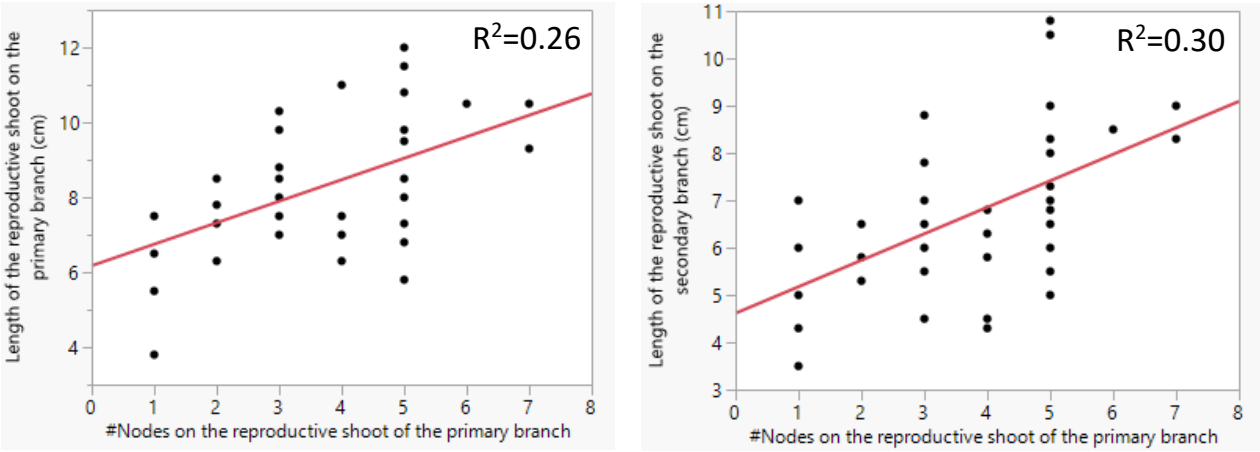

Figure A7. Left: scatter plot of correlation between the number of nodes on the reproductive part of the primary shoot and the length of the reproductive part of the primary shoot. Right: scatter plot of correlation between the number of nodes on the reproductive part of the primary shoot and the length of the reproductive part of the secondary shoot.

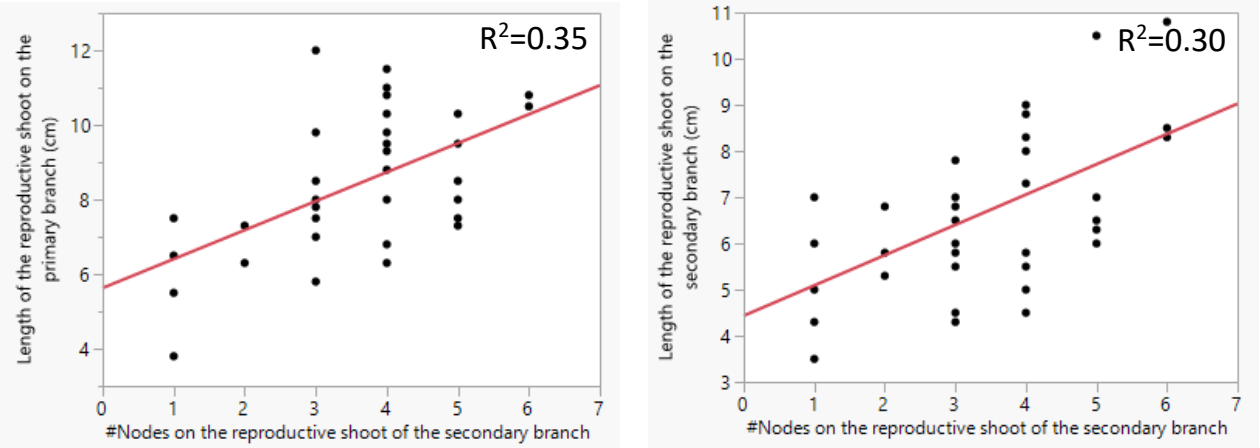

Figure A8. Left: scatter plot of correlation between the number of nodes on the reproductive part of the secondary shoot and the length of the reproductive part of the primary shoot. Right: scatter plot of correlation between the number of nodes on the reproductive part of the secondary shoot and the length of the reproductive part of the secondary shoot.

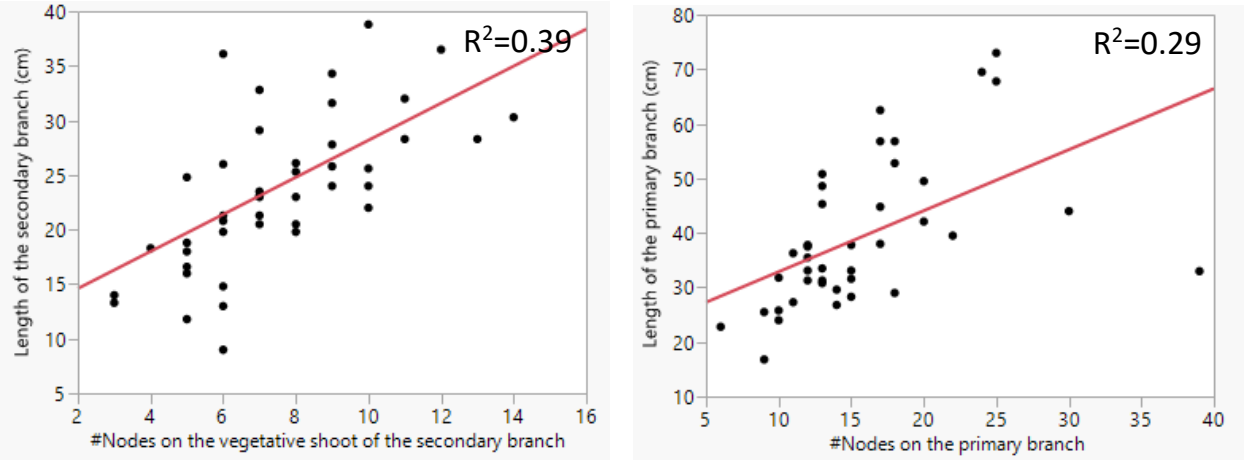

Figure A9. Left: scatter plot of correlation between the number of nodes on the vegetative part of the secondary shoot and the length of the secondary shoot. Right: scatter plot of correlation between the number of nodes on the primary shoot and the length of the primary shoot.

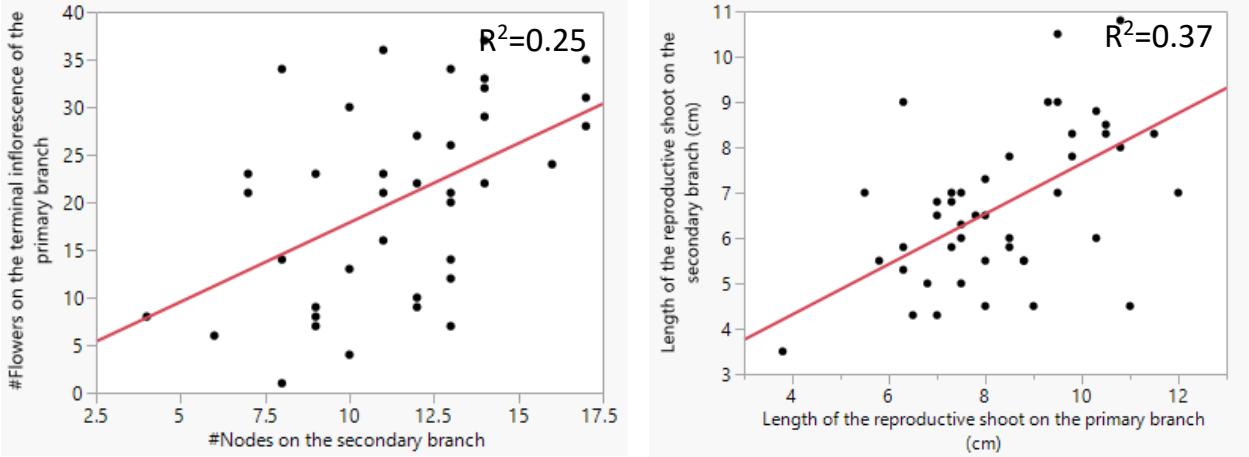

Figure A10. Left: scatter plot of correlation between the number of nodes on the secondary shoot and the number of flowers on the terminal inflorescence of the primary shoot. Right: scatter plot of correlation between the length of the reproductive part of the primary shoot and the length of the reproductive part of the primary shoot.

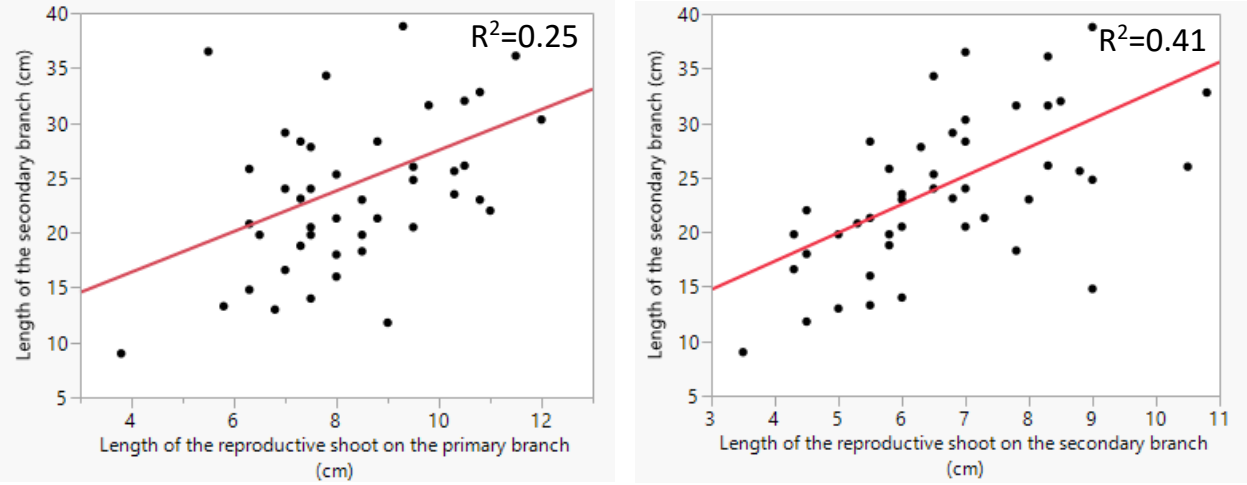

Figure A11. Left: scatter plot of correlation between the length of the reproductive part of the primary shoot and the length of the secondary shoot. Right: scatter plot of correlation between the length of the reproductive part of the secondary shoot and the length of the secondary shoot.

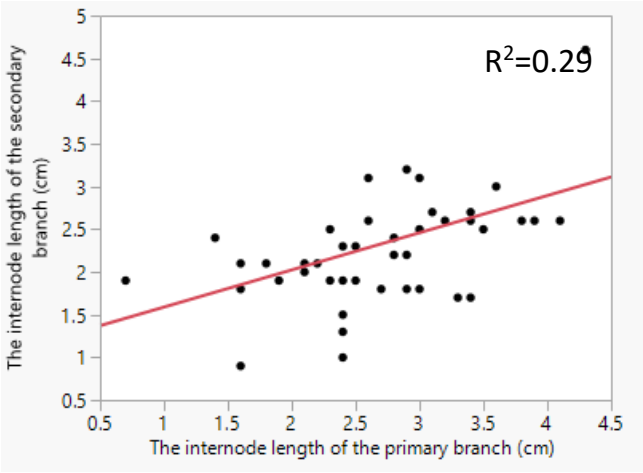

Figure A12. Scatter plot of correlation between the internode length of the primary shoot and the internode length of the secondary shoot.