GENETIC ANALYSIS OF EARLINESS TRAITS IN CHICKPEA (*CICER ARIETINUM* L.)

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Abstract

The latter part of the reproductive growth phase in chickpea (*Cicer arietinum* L.) often coincides with declining temperature and wet conditions in western Canada, in sharp contrast to many other growing environments. This exacerbates the indeterminate nature of the crop, leading to excessive canopy development, and subsequently resulting in delayed maturity. The objectives of this study were to: i) determine the genetic relationships of short internode, double podding and early flowering traits with earliness of crop maturity; ii) determine the genetic control of major earliness traits in chickpea; iii) assess the patterns of post-flowering dry matter accumulation and partitioning to reproductive parts as related to earliness.

The results showed that double podding significantly reduced the number of days taken to maturity, under the conditions where this trait was sufficiently expressed. The best double podding genotypes, i.e. those with 15—35% of the podded nodes bearing double pods, were about one week earlier than their single podding counterparts and standard checks. A physiological study revealed that the double podding parental genotype 272-2 partitioned a relatively greater proportion (about 58%) of the total dry matter to pods compared to 42—54% in the single podding genotypes. Double podding increased the total number of pods set, and thus the increased demand for assimilates may have precluded further production of stems and leaves, resulting in an earlier transition of reproductive growth to physiological maturity. Days to flowering was positively associated with days to maturity, and partial path analysis revealed that days to flowering contributed to days to maturity indirectly via days to first pod maturity.

Days to flowering explained 32% of the variation in days to first pod maturity. However, the short internode trait had an undesirable effect, in that all the short internode segregants were too late to mature.

Genetic studies revealed that days to flowering was determined by two major genes plus polygenes in chickpea in the short-season temperate environment of western Canada. The two major genes control over 65% of the phenotypic variation. Also, the additive component of genetic variance was significant for days to first podding, days to first pod maturity, reproductive period, and days to maturity; which is desirable for development of superior inbred cultivars of chickpea. These key phenological traits are interrelated but could be manipulated separately in the breeding process. Additional gain in earliness of crop maturity may be achieved through combined selection for these traits.

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Abbreviations and Acronyms

ARCBD - Augmented randomized complete block design

CDC - Crop Development Centre, University of Saskatchewan

CGIAR - Consultative Group on International Agricultural Research

FAO - Food and Agricultural Organization

ICARDA - International Center for Agricultural Research in the Dry Areas

ICRISAT - International Crops Research Institute for the Semi-Arid Tropics

RCBD - Randomized complete block design

RILs - Recombinant inbred lines

AIC - Akakie information criterion

EIM - Expectation and iterated maximization

GA - Genetic advance

GCV - Genetic coefficient of variation

h^2 - Heritability (narrow sense)

H^2- Heritability (broad sense)

JSA - Joint segregation analysis

QTL - Quantitative trait loci

MG5 - Multiple generations five, P_1, F_1, P_2, F_2 $F_{2:3}$

1. Introduction

Chickpea (*Cicer arietinum* L.) is an annual grain legume crop grown mainly for human consumption. It plays an important role in human nutrition as a source of protein, energy, fiber, vitamins, and minerals for large population sectors in the developing world and is considered a healthy food in many developed countries (Jodha and Subbarao, 1987; Maiti, 2001). In addition to its high protein content (22─28%), chickpea is a good source of essential amino acids such as tryptophan and lysine (Awasthi et al., 1991; Hulse, 1991). According to Singh et al. (2000), chickpea is richer in calcium and phosphorus content than most other pulse crops. Chickpea seeds are low in anti-nutritional factors like tannins, alkaloids or enzyme inhibitors, which are known to be problems in some other pulse crops (Williams and Singh, 1987).

Chickpea was introduced to western Canada only recently and field production began in the late 1990s. Since then the area under chickpea production increased sharply reaching a peak of about 450, 000 ha in 2001 (Saskatchewan Agriculture and Food, 2003). However, the area of production decreased substantially in 2002─2004, owing to high disease pressure of ascochyta blight and problems associated with late maturity. Chickpea area increased somewhat in 2005 (Saskatchewan Agriculture and Food, 2006a) and is expected to rise further in 2006 due to high prices for the kabuli market class. This crop is grown mainly for the export market, and Canada has become

one of the major exporters within the short history of chickpea cultivation in the country (Saskatchewan Pulse Growers, 2000). Canada, which has a comparative yield advantage of about 1510 kg ha^{-1} as compared to the 820 kg ha^{-1} world average yield of chickpea (FAO, 2005), could continue to hold a large share in the international chickpea export market. There is also a large potential for local uses of Canadian chickpea as a healthy food and as a feed for livestock.

In its traditional production environments including the Mediterranean, South and western Asia and East Africa, chickpea matures under progressively declining soil moisture and increasing temperature conditions that enforce maturation and facilitate crop harvesting (Khanna-Chopra and Sinha, 1987; Kumar and Abbo, 2001). However, chickpea production faces unique challenges in the new environment in western Canada in that the maturity phase of the crop coincides with declining temperatures, often moist early fall conditions and declining autumnal day length. These conditions encourage continued growth and formation of new flowers and pods in chickpea, a species which has a highly indeterminate growth habit (Singh, 1987; van Rheenen et al., 1994). Satisfactory maturation of pods does not occur under these conditions, and the crop is often exposed to freezing temperatures prior to maturity, resulting in reduced yield and quality.

The length of the growing season in western Canada is delimited between late spring and early fall frosts for chickpea, such that no significant window exists to extend the length of the growing period to meet the requirement of a long growing season in this crop (Miller et al., 2002). Early crop maturity is essential to match crop duration with the period of favorable growing conditions, to avoid losses caused by

early fall frost in the Prairies, and to stabilize yield and quality. Earliness is also important for management factors associated with mechanized harvesting in chickpea.

Progress in chickpea breeding has been constrained by the lack of satisfactory genetic sources of early maturity in the short-season temperate environment of western Canada. Some earlier maturing chickpea varieties were developed for western Canada, but even these often take longer to mature than the length of the growing season in the area. It was hypothesized that early maturity in chickpea in western Canada could be achieved through three simply inherited genetic traits, i.e. short internode, double podding and early flowering. Favorable single genes like these have, in some instances, brought about major achievements in plant breeding; for example, dwarfing genes in wheat (*Triticum aestivum* L.) (Athwal, 1971), and genes for determinate/semi-determinate growth habit in soybean (*Glycine max* (L.) Merr.) (Bernard, 1972).

Short internodes in chickpea may contribute to early maturity without a negative effect on grain yield by reducing excessive canopy growth during wet seasons, and correspondingly by increasing the proportion of assimilates partitioned into grain. Chickpea generally bears one pod per peduncle. However, some accessions bear two pods per peduncle at some nodes (Sheldrake et al., 1978; Pundir et al., 1988). This double podding characteristic increases the total number of pods set and the sink demand that could hasten the switch to maturation phase. Time to flowering, through its effect on the onset of reproductive growth, may generally be important for earliness of crop maturity in chickpea. Early flowering triggers early pod setting and may enable these pods to reach physiological maturity in a timely manner (Or et al., 1999). Pyramiding the alleles for short internode, double podding and early flowering through

breeding may produce genotypes with the desired level of earliness in chickpea in western Canada.

Breeders could deploy available means to develop early maturing varieties, but success in breeding depends upon our understanding of the genetic and physiological bases of earliness traits. According to Kumar and Abbo (2001), lack of genetic knowledge is mainly responsible for the slow progress in chickpea breeding in general. The utilization of genetic and physiological information will allow breeders to employ improved strategies to be able to make substantial progress in reducing the requirement of a long growing season in chickpea in western Canada. Therefore, an understanding of the physiological and genetic bases of earliness of crop maturity and conceptualizing genetic strategies of reducing crop duration under this environment should enable breeders to better bridge the gap between the apparent and desired level of earliness in chickpea in western Canada. Thus, the objectives of this study were:

1. to determine the genetic relationships of short internode, double podding and early flowering traits with duration of crop maturity in chickpea in western Canada;
2. to determine the genetic control of major earliness traits in chickpea in this environment;
3. to assess the growth and developmental patterns of diverse chickpea genotypes as related to the timing of crop maturity.

2. Literature Review

2.1 Production Trends of Chickpea

Chickpea ranks third among the world pulses after dry bean (*Phaseolus vulgaris* L.) and pea (*Pisum sativum* L.) in production (FAO, 2005). Currently, it covers 15.3% (11.2 million ha) of the area and accounts for 14.9% (9.2 million metric tonnes) of the production of pulse crops in the world (FAO, 2005). This crop is grown in over 35 countries in the world in South Asia, West Asia, North Africa, East Africa, southern Europe, North and South America, and Australia (Jodha and Subbarao, 1987; Singh, 1993). The ten top producing countries in order of importance are India, Turkey, Pakistan, Iran, Mexico, Myanmar, Ethiopia, Australia, Spain, and Canada; of which India accounts for over 65 % of the total global chickpea production (FAO, 2005).

Global chickpea production has more or less remained constant since the 1960s (van Oppen and Parthasarathy Rao, 1988; Rees et al., 2000). There has been a decline in the area sown to chickpea in India and Pakistan, but this decline was compensated for by a rise in production in Turkey and, more importantly by new producers such as Australia and Canada (van Oppen and Parthasarathy Rao, 1988; Bayaner and Uzunlu, 2000; Kumar and Abbo, 2001). Lovett and Gent (2000) projected that further increase in global chickpea production is likely to occur through increased productivity. A relatively high capacity and investment in chickpea research in the newly emerged

producing countries, as well as at the CGIAR centers ICRISAT and ICARDA, should generate chickpea production technologies that enable an increase in productivity.

Chickpea is an integral part of the daily diet of large population sectors in South Asia, West Asia, North and East Africa and southern Europe (Jodha and Subbarao, 1987; Williams and Singh, 1987; Abbo et al., 2003). At present the demand for chickpea is higher than its current production, especially in south and west Asian countries, Spain and some northern African countries (Singh, 1997; Lovett and Gent, 2000; Kumar and Abbo, 2001). With continued population growth, the demand for high protein, high energy crops such as chickpea will also grow (Oram and Agacoili, 1994; Kothari, 2000; Lovett and Gent, 2000; McGreevy, 2000). The international trade in chickpea is expected to rise in the future. Canadian chickpea production could play a significant role in meeting some of the growing demand for this crop globally.

2.2 Adaptation of Chickpea to Western Canada

In western Canada chickpea is grown mainly in the Brown and Dark Brown soil zones in central and southwestern Saskatchewan and southeastern Alberta. In Saskatchewan, about 70% of the chickpea area is in the Brown soil zone (Saskatchewan Agriculture and Food, 2003). However, average yield was slightly higher in the Dark Brown soil zone, especially in dry seasons such as 2003 (Saskatchewan Agriculture and Food, 2004). This indicates that the Dark Brown soil zone is also a potential area for expansion of chickpea production in Saskatchewan. However, chickpea does not tolerate waterlogging and is not well-suited to excessively wet soils as in the Black soil zone in the province.

Saskatchewan has a large cultivated farm land area covering over 18.5 million ha (Saskatchewan Agriculture and Food, 2004), providing opportunity for expansion of chickpea production in the province. The climate of the province, characterized by cold winters and dry summers, limits disease and insect problems of the chickpea crop. The most internationally widespread chickpea disease, ascochyta blight (*Ascochyta rabiei*), occurs in all regions of Saskatchewan. However, other important chickpea diseases including wilt/root rot complex and stunt virus are not a problem in western Canada, thus providing an advantage to chickpea production in the region. The scarcity of most diseases would allow the Canadian chickpea industry to remain competitive globally.

Chickpea has good drought tolerance (Saxena et al., 1993), making it well suited to the semi-arid regions in the Prairies. Indeed chickpea is one of the few crops that can produce sustainable yield in relatively harsh environments (Kumar and Abbo, 2001). Inclusion of chickpea and other leguminous crop in the cereal-based intensive cropping system of western Canada provides multidimensional benefits to the farming system. As a leguminous crop, chickpea fixes atmospheric nitrogen (N) through biological nitrogen fixation (Rupela and Saxena, 1987). Growing chickpea in a rotation with cereals also provides an opportunity to control some grassy weeds that are often difficult to control within cereals (Muehlbauer, 1996). Chickpea and other pulses are competitive compared to other crops in the rotation providing a relatively high return over variable expenses in the semiarid regions in western Canada (Saskatchewan Agriculture and Food, 2006b).

As a new crop to western Canada, chickpea faces a unique challenge in this environment. It is the only region in the world where the crop often matures in cool,

moist conditions with declining autumnal day length. Given the highly indeterminate nature of the species, this condition encourages continued growth and formation of new flowers and pods that consequently delays maturity and exposes the crop to early fall frost damage. Many of the growing seeds remain unfilled, affecting yield and quality of the crop to a great extent.

Successful production of chickpea in western Canada requires use of genotypes with early maturity characteristics in addition to resistance to ascochyta blight. These two constraints have received by far the most attention in chickpea breeding for Saskatchewan. Early maturity is an important strategy of matching crop duration with the period of favorable growing conditions to minimize the impact of frost damage. Early maturity has major adaptive significance in chickpea in western Canada. Also, reducing the duration of crop growth in chickpea will increase and stabilize yield to a great extent.

2.3 History of Chickpea Domestication and Adaptation Constraints

Chickpea is believed to have originated in the present-day southeastern Turkey (Ladizinsky and Adler, 1976; van der Maesen, 1987). From this region, chickpea spread southeast as well as to the western hemisphere early in the history of its domestication. Chickpea has been grown for millennia in the Indian subcontinent and east Africa in the east, and introduced more recently to Chile, Mexico and California in USA in the west (Jana and Singh, 1993; Kumar and Abbo, 2001). It is evident from this that chickpea has been traditionally grown in only the tropical and subtropical regions of the world.

The main environmental constraints to chickpea production in the traditional growing environments are drought, and to a lesser extent salinity and deficiency in mineral nutrients (Saxena et al., 1993; Singh, 1993; Singh et al., 1994; Subbarao et al., 1995). The chickpea crop relies on residual soil moisture in major growing areas such as India and Ethiopia without supplemental irrigation that regularly exposes the latter part of the crop's growth to terminal drought (Saxena, 1987; Kumar and Abbo, 2001; Anbessa and Bejiga, 2002). Heat is also a problem in some areas (Singh, 1993), which causes atmospheric desiccation and escalation of the drought stress.

Millennia of chickpea cultivation in drought-prone environments shaped the crop towards better adaptation to the constraints and resources of these environments (Kumar and Abbo, 2001). For example, chickpea is a highly indeterminate species, which gives it an adaptive advantage in environments where intermittent drought prevails and where site to site or year to year weather fluctuations are high (Maiti, 2001). Unfortunately the allele for determinate growth habit, which played a key role in the improvement of other grain legumes such as soybean (Bernard, 1972) and common bean (Singh, 1982), is lacking in chickpea. Determinate growth habit might have been selected against during the spread and establishment of the chickpea crop in the low latitude areas. The loss of such a major adaptive trait would affect the rate of adaptation of this crop to new environments such as western Canada. The allele for determinate growth habit in chickpea could be reinstated through induced or natural mutation (van Rheenen et al., 1994).

In addition to the factor of latitude of origin and the traditional area of cultivation, studies suggested that the process of chickpea domestication also posed

unique limitations on genetic variability within the cultivated chickpea (Abbo et al., 2003; Berger et al., 2003). Abbo et al. (2003) provided evidence that chickpea domestication occurred at a single point and time, while the other west Asian crops such as wheat and barley (*Hordeum vulgare*) have multiple points of domestication. As a consequence, relatively low alleic variations were captured in chickpea during the domestication process. Berger et al. (2003) reported that the geographic distribution of the wild progenitor of chickpea, i.e. *Cicer reticulatum* Ladiz., is relatively narrow compared to that of wheat, barley or pea. The wild chickpea species is found only in a limited area in southeastern Turkey, between latitudes of 37.3─39.8^{O}. Thus, *C. reticulatum* and subsequently the cultivated chickpea, C. *arietinum*, can harbor only limited genetic variation for breeding.

Probably because of the risk of ascochyta blight, chickpea cropping was shifted from winter to spring sowing early in the crop's history (Abbo et al., 2003). The current growing practice of the cultivated chickpea is different from the autumn germination and spring flowering of its wild progenitor, *C. reticulatum* in southeastern Turkey, and this has further narrowed its genetic base (Abbo et al., 2002). These authors speculated that with the shift to summer cropping some adaptive traits like the alleles for vernalization, which are present in the wild progenitor, have been lost. These alleles are needed in the cultivated chickpea to delay flowering in environments where early pod setting is constrained by cooler temperature (Singh, 1997). The alleles for vernalization response could be incorporated into the cultivated chickpea through crosses with the wild species *C. reticulatum*.

Significant genetic erosion has also occurred in chickpea over the years due to diseases, insects, and environmental stresses (Croser et al., 2003). Chickpea has been relegated to less fertile lands in many growing areas over the last 4─5 decades for economic and strategic reasons. The Green Revolution promoted the use of high input cropping systems, and chickpea and some other crops were pushed to marginal areas, particularly in the developing world (Croser et al., 2003). This resulted in the loss of some ecotypes, further minimizing the genetic variation in the genus.

As a combined effect of all the above-mentioned causes, chickpea germplasm displays low genetic variability compared to other self-pollinated crops (Croser et al., 2003). Studies conducted over the past few decades confirmed that the levels of genetic polymorphism in chickpea were low using karyotypic studies (Ohri and Pal, 1991), seed storage proteins (Ladizinsky and Adler, 1976), isozyme variability (Ahmad and Slinkard, 1992), and DNA markers (Simon and Muehlbauer, 1997). As a result, sources of some important traits may be lacking in the chickpea germplasm. This hampers efforts to identify sources of resistance to biotic and abiotic stresses and perhaps places limitation on adaptation range of the crop.

2.4 Breeding for Early Maturity in Chickpea: Gene Pool Considerations

2.4.1 Exploitation of wild progenitors of chickpea

The cultivated chickpea belongs to the genus *Cicer*. This genus comprises 43 species of which 34 are perennial and 9 are annual (Ladizinsky and Adler, 1976; van der Maesen, 1987). Only one species, *C. arietinum,* is cultivated among these.

According to Ladizinsky (1995), all annual chickpea species and some perennials are diploids and have chromosome number 2n = 16. Interrelationship studies among the *Cicer* species, based on hybridization success, storage proteins and DNA markers, have showed that *C. reticulatum* and *C. echinospermum* are the wild species most closely related to the domesticated *C. arietinum* (Kazan and Muehlbauer, 1991; Ahmad and Slinkard, 1992; Singh and Ocampo, 1993). There seems to be a consensus that *C. reticulatum* is the primary progenitor, while *C. echinospermum* is the secondary wild progenitor of the cultivated chickpea (Ladizinsky and Adler, 1976; Ahmad and Slinkard, 1992).

The gene pools of most crop plants have less variability compared to the naturally occurring genetic variation of their wild progenitors. The genetic variability of the wild *Cicer* species could be used for the improvement of the cultivated chickpea, especially where sources of genes for adaptation to new environments like western Canada are critically required. Singh et al. (1995) and Croser et al. (2003) showed availability of sources of resistance to several abiotic (cold, drought) and biotic (ascochyta blight, fusarium wilt, botrytis grey mould) stresses in wild *Cicer* species. Further, Singh and Ocampo (1997) found broad variation and numerous transgressive segregants in economically important traits in F_2 populations derived from crosses between *C. arietinum* and *C. reticulatum* and between *C. arietinum* and *C. echinospermum*. These authors suggested that genes from the wild species when introgressed into a cultivated background may have positive effects on growth and yield. However, there are only 116 accessions of wild annual *Cicer* species collected

and evaluated thus far , and as a result these species provided a limited benefit for the improvement of the cultivated chickpea (van der Maesen, 1987; Berger et al., 2003).

A major challenge to the utilization of wild *Cicer* in the improvement of the cultivated chickpea is the technical difficulty in obtaining hybrid seeds from interspecific hybridizations (Croser et al., 2003). Interspecific hybridizations have resulted in fertile F_1 hybrids between *C. arietinum* and *C. reticulatum* (Ladizinsky and Adler, 1976; Singh and Ocampo, 1993) and at least partial success has been achieved from crosses between *C. arietinum* and *C. echinospermum* (Singh and Ocampo, 1997). However, researchers have been unable to produce hybrids between the cultivated species and the remaining species, particularly with the perennials (Singh, 1987). Perennial x annual crosses have been possible at least in *Medicago* (Sangduen et al., 1982) and ryegrass (Warnke et al., 2002), and this will probably work for chickpea if improved techniques are used. Croser et al. (2003) suggested that techniques such as 'embryo rescue' and 'protoplast fusion' may be used as alternative strategies to enable transfer of useful genes from relatively distant wild species to the cultivated chickpea. Efforts are underway to optimize tissue culture

2.4.2 Desi-kabuli introgression

Two main types, also called 'market classes', are recognized within the cultivated chickpea (Singh, 1987; Maiti, 2001). The first is the 'desi' type which constitutes over 80% of the total chickpea production (Singh, 1987). This type has angular seed shape and varying in color from black to pale brown or green. It is mainly grown in the Indian subcontinent and East Africa and some parts of the Middle East

(Gil and Cubero, 1993; Jana and Singh, 1993). The second type is known as 'kabuli' which is rams-head shaped, with cream to white colored seed. It is native to the Mediterranean countries (Gil and Cubero, 1993; Jana and Singh, 1993). According to Jana and Singh (1993), there are strong consumer preferences for one or the other that might be responsible for the regional differentiation between desi and kabuli chickpea.

Cluster analysis by Bahl et al. (1990) suggested that kabuli and desi types are distinct groups within the cultivated taxon. It is generally believed that the kabuli type evolved recently from the more primitive desi type (Hawtin and Singh, 1980; Maiti, 2001). However, based on evidence from introgression with *C. reticulatum*, Pundir et al. (1984) suggested that the kabuli and desi types may have originated independently from this wild progenitor.

Desi-kabuli introgression opens a possibility for the potential utilization of genetic diversity conserved in different geographic areas (Knights, 1980). Intercross between the two types may aid researchers in identifying more suitable types of plants with respect to yield and earliness. Through this process desirable characters such as tall stature and large seed size from kabuli chickpea, and a greater number of pods per plant and seeds per pod as well as early maturity from the desi type could be combined into a single genotype (Bahl, 1980; Knights, 1980). Gowda et al. (1987) obtained a wide range of segregants in the F_2 of desi x kabuli crosses for seed shape, size and color. Further, a greater variation was observed in desi x kabuli crosses than either desi x desi or kabuli x kabuli crosses in yield and yield related traits (Maynez et al., 1993). However, as is often the case with wide crosses, many of the segregants from desi x kabuli crosses are intermediate in seed color and shape and are commercially

undesirable. Larger population size or making backcrosses to either the desi or kabuli parent may help to recover useful transgressive segregants in such crosses (Hawtin and Singh, 1980). It may require a few generations of backcrossing to either parental type to acquire proper quality.

2.4.3 Exploitation of alien germplasm

A number of national and international organizations have collected and assembled primitive landraces or farmers' varieties of chickpea over the last century. The largest collection containing about 16,000 accessions is held at ICRISAT, India (Pundir et al., 1988). ICARDA also holds over 6,000 kabuli accessions and over 100 entries of wild species of chickpea (Singh et al., 1991). In Canada, the Plant Gene Resource Unit based in Saskatoon holds 588 chickpea accessions acquired from different sources (A. Diederichsen, personal communication).

South Asia and the Mediterranean are considered the primary centers of diversity for chickpea, while Ethiopia is a secondary center of diversity (van der Maesen, 1987; Upadhyaya, 2003). This implies that the greatest amount of genetic diversity is found in these areas. However, useful germplasm for improving the adaptation and performance of chickpea in the western Canadian environment could also be found with systematic introduction and evaluation of chickpea landraces originating from similar growing environments. Materials from higher latitude environments in northern India, China or the former USSR regions could prove beneficial as sources of adaptive genes for improvement of chickpea in western Canada. The chickpea growing regions in China have similar climatic pattern as the Prairies (Y.

Gan, personal communication), and it is possible that suitable materials can be found from there. Extensive evaluation of germplasm from these areas under western Canadian conditions is needed to identify sources of adaptive traits to this environment.

2.5 Physiological and Genetic Basis of Earliness in Chickpea

2.5.1 Dry matter production and partitioning and timing of crop maturity

During their life cycle, plants accumulate dry matter in stems, leaves, roots, and reproductive organs and simultaneously pass through a succession of phenological events. These two interdependent processes are termed as growth and development, respectively. Khanna-Chopra and Sinha (1987) recognized four major developmental stages in chickpea including germination, seedling growth, flowering and early pod development, and maturation. The rate of progress through these events and eventually crop growth rate determine the duration of crop growth and the adaptation of genotypes to a particular environment. A thorough understanding of the growth and developmental pattern of the chickpea crop, as well as the impact of various environmental factors on crop growth and development are therefore essential for effective manipulation of the duration of crop maturity and crop-environmental adaptation.

Dry matter accumulation in chickpea follows a typical sigmoidal curve, with a slow rate at the early vegetative phase followed by a rapid rate of increase during flowering/podding and a decreasing trend towards the end of the season (Guhey and Trivedi, 2001). However, O'Toole et al. (2001) noticed differences among chickpea

genotypes in their relative rates of dry matter accumulation at different growth stages. Genotypes with a rapid rate of growth may result in earlier flowering, pod initiation and finally, crop maturity (Lather et al., 1997).

As a highly indeterminate species, chickpea typically continues to grow and develop flowers and pods as long as there are favorable conditions for growth (Khanna-Chopra and Sinha, 1987). This will lead to excessive canopy development and simply delay maturity with no benefit to yield or rather with a negative effect on yield due to reduced partitioning. Limited post-flowering growth in vegetative parts is desired in environments where growing conditions allow excessive vegetative growth and delay maturity (van Rheenen et al., 1994). Differences may exist for degree of post-flowering vegetative growth among chickpea germplasm. For example, Shamsuzzaman et al. (2002) observed that an early maturing chickpea mutant 'Hypersola' had significantly lower amounts of leaf and stem dry matter during its last few weeks of growth as compared to its parental genotype. This characteristic reduces the degree of indeterminacy of the crop and thus allows early maturation.

The manner and priority with which dry matter is partitioned to the reproductive parts is an important factor for adaptation and yield of crop plants (Wallace, 1985). Williams and Saxena (1991) reported that some chickpea genotypes established the vegetative frame necessary for light capturing before flowering and then partition most subsequent dry matter to pods. This efficient partitioning system is a desirable characteristic limiting excessive canopy development in the cool and wet environment as in western Canada. This also increases harvest index and subsequently grain yield.

2.5.2 Genetics of earliness traits in chickpea

Genetic studies on chickpea lag far behind its economic importance and that lack of genetic knowledge is partly responsible for the relatively less advance in chickpea breeding (Kumar and Abbo, 2001). Genetic information can be used to formulate the most efficient breeding strategy for developing early maturing genotypes (Upadhyaya and Nigam, 1994). Also, the estimates of different components of variance (additive, dominance and epistasis) are important to predict the probabilities of obtaining transgressive segregants (Khattak et al., 2001).

Genetic analysis in chickpea showed that the trait of days to flowering was predominantly under the control of additive genetic variance (Gowda and Bahl, 1978; Singh et al., 1992; Singh et al., 1993; Kumar et al., 1999) while both additive and nonadditive variance components were important for days to maturity (Singh et al., 1993). However, Bhardwaj et al. (2005) reported that the additive component of variance was higher in magnitude than the dominance component for days to maturity as well. Kidambi et al. (1988) found that duplicate epistasis is important for both days to flowering and maturity, whereas Bhardwaj et al. (2005) showed that an additive-dominance model was adequate for days to maturity in chickpea. The differences could be attributed to the environment and genetic population used. Further study is needed to more completely establish the genetic basis of early maturity in chickpea. This is especially important under western Canadian condition where genetic information is lacking and daylength-temperature regimes are so different compared to those experienced by the crop throughout its range of production.

2.6 Early Maturity Strategies in Chickpea

Early maturity is an important agronomic trait in chickpea in western Canada. It is a strategic objective in germplasm development for this environment. Early maturity minimizes risk of frost damage and enables producers to attain better harvest quality and a higher yield. Early maturing genotypes need to be developed and commercialized for more consistent production, better quality and ultimately greater export market share for Canadian chickpea. Early maturity can be achieved through one or more of the following strategies.

2.6.1 Determinate growth habit

Cereals are determinate in their growth habit and show a complete switch to reproductive mode after heading, whereas legumes generally continue to grow vegetatively even after the beginning of flowering and podding. Some legumes such as soybean and common bean show a determinate growth habit (Bernard, 1972; Singh, 1982). Yet determinacy in legumes is not the same as in cereals. Determinate legumes complete flowering and podding in a shorter span of time than indeterminate types, but do not completely stop vegetative growth upon flowering as in cereals.

Determinacy in many crops is under simple genetic control. For example, interaction of two stem termination genes regulates determinate, semi-determinate and indeterminate growth habits in soybean (Bernard, 1972). The determinate growth habit is not available in chickpea germplasm. Van Rheenen et al. (1994) reported an induced determinacy in chickpea through mutation, but this mutant was indeterminate when grown in Saskatchewan. The allele for determinate growth habit might have been

selected against during millennia of chickpea cultivation in semi-arid environments, where an indeterminate growth habit is important to cope with intermittent drought.

The determinate trait, besides its benefit as a component of the bushy growth habit, also shortens the harvest period at least in some genetic backgrounds (Kwak et al., 2006). Stem termination genes, by reducing apical dominance, would allow more bottom branching. A larger numbers of bottom branches, in turn, would produce more flowers and pods in a short time span. Through this, a determinate habit allows a relatively early and uniform maturation of pods.

However, complete determinacy may also have undesirable consequences. Determinacy may reduce plant height and leaf area and subsequently limit the potential for biomass production and grain yield. In bean, although determinate genotypes tend to be earlier in maturity than indeterminate genotypes, the former generally have lower yield potential and show less yield stability (Cerna and Beaver, 1990). It is probably preferred to develop a more determinate type of chickpea rather than complete determinacy so as to allow the flexibility to exploit well the available soil moisture and maximize yield in drier seasons.

2.6.2 Short internode

Genotypic variation in internode length has been observed in a wide array of plants including lentil (Ladizinsky, 1997) and pea (Reid and Ross, 1993), which are botanically related to chickpea. In pea, where the studies are sufficiently extensive, a considerable number of internode length mutants have been reported and corresponding alleles were identified (Reid, 1986; Cramp and Reid, 1993). All the mutations are

recessive and when homozygous recessive alleles are present in a single plant, they cause substantial reduction in internode length. For example, the internodes of *lkc* (one of the dwarfing alleles in pea) plants are 30─40% shorter than those of comparable *Lkc* plants (Reid et al., 1991), and this is attributed to reductions in both cell length and number of cells per internode.

In chickpea, a phenotypically distinct dwarf type E100Ym with short internodes was identified at ICRISAT (Dahiya et al., 1984). It was described as a macromutant having a number of distinct characters including small, thick and deep green leaves, and pink flower color (Sandhu et al., 1990). An inheritance study showed that the short internode trait in this genotype is controlled by a single recessive gene (Sandhu et al., 1990). Therefore, this allele could easily be used in chickpea breeding.

Dwarfing genes may act by altering gibberellic acid level and form, like the *Rht* gene in wheat (Keyes et al., 1990). However, Reid et al. (1991) showed that dwarfism in the pea mutants indicated above was not due to modified gibberellic acid levels as determined by gas chromatography. Short-internode plants were not as responsive as the wild-type to applied gibberellins either. They suggested that the short stature of pea plants was perhaps the result of a direct or indirect interference with the transduction of the gibberellin signal. Further evidence indicated the involvement of indole-3-acetic acid in plant dwarfism in pea, such that an indole-3-acetic acid level below that necessary for normal elongation leads to a reduced stature (McKay et al., 1994). In lentil, when the dwarf segregants and their parental lines were grown in the dark, they had the same internode length (Ladizinsky, 1997). It appears that short internode is regulated by different mechanisms, depending upon species (wheat, pea or lentil) and

the mutant allele. A more sufficient understanding is needed if internode length is to be manipulated in a directed fashion.

Dwarfing genes have provided a significant contribution in the improvement of many economically important crops including wheat and rice (Athwal, 1971). The main advantage for utilization of short internode in a chickpea breeding program is to reduce overgrowth in canopy structure and improve the proportion of assimilates partitioned into grain. Theoretically, this will result in increased grain yield. Dahiya et al. (1990) reported that medium height chickpea recombinants from a cross between E100Ym, a bushy dwarf mutant with short internodes, and conventional types showed better performance compared to the parents for total number of pods per plant, seed yield and biological yield. A potential additional benefit could be a reduction in the time taken to enlarge and produce more internode cells and hypothetically earlier maturity. Davis (1974) obtained short-statured, earlier maturing and more productive cotton hybrids as a result of semi-dwarf alleles contributed from one of the parents. Shortened internode plants are relatively compact and may facilitate mechanical harvesting as well.

2.6.3 Double podding

The variants in number of pods per reproductive node in chickpea germplasm include a single pod per peduncle, two pods per peduncle and multiple pods per peduncle (Pundir et al., 1988; Gaur and Gour, 2002). The majority of the available chickpea germplasm accessions have only one pod at each peduncle, and only a few had double pods. Srinivasan et al. (2005) reported that out of the 12,018 chickpea

germplasm accessions evaluated at ICRISAT, only 100 were double podding. The double podding trait in chickpea is governed by a single recessive gene *ss*, indicating that this trait can easily be incorporated into the desired genetic backgrounds (Kumar et al., 2000).

Complete double podding is not observed in chickpea. Typically, only a portion of the nodes produce two pods per peduncle, while the other nodes bear only one pod per peduncle. The expressivity of double podding (i.e. percentage of double podded nodes to the total pod bearing nodes) seems to vary with growing conditions and genotype. Kumar et al. (2000) reported that genotype JG 62 had 8─31% of nodes with double podding when planted early, and 17─69% nodes with double podding when planted late. They also found that the expressivity of double podding ranged from 1.1─14.8% among F_2 individuals derived from a cross between the single podding genotype ICCV 2 and the double podding genotype JG 62. However, the genetic basis of this variation is not clear.

The double-podding trait is known to enhance seed yield in chickpea. Sheldrake et al. (1978) reported that the double podding character conferred a 6─11% yield advantage under conditions in which the character was highly expressed. The double podding trait produced higher seed yield under soil moisture stress conditions, common in chickpea production regions (Kumar et al., 2000). The allele for double podding also had a positive effect on the stability of seed yield (Rubio et al., 1998). The contribution of the double podding trait to yield stability might have stemmed from its involvement in inducing earliness. Kumar and Rao (2001) reported that an early flowering and double podded chickpea genotype ICCV 96029 matured early, which could be due to

the combined effect of the two characters. The increased number of pods per peduncle and subsequently higher total pod set may increase demand for photosynthate resulting in an earlier transition to physiological maturity.

Gaur and Gour (2002) identified chickpea genotypes that produce 3─9 flowers per peduncle at many flowering nodes in the F_2 generation of an interspecific cross ICC 5783 (*C. arietinum* L.) and ICCW 9 (*C. reticulatum* Ladiz.). They also found that this multi-podding trait was controlled by a single recessive gene independent of the double podding locus. The benefit of multi-podding compared to double and single podding is yet to be determined. Multi-podding could be a good strategy to improve yield and earliness of crop maturity in chickpea.

2.6.4 Early flowering

Time to flowering, taken as the number of days from seeding to onset of flowering, usually varies with local circumstances, such as sowing date, altitude and latitude. In chickpea genotypes, time to flowering was influenced by the seasonal temperature profile and the photoperiodic response of the plant with no interaction between the two factors (Summerfield and Roberts, 1988). Differences in time to flowering are, therefore, observed as a result of differences in temperature levels and day lengths obtained from different locations, seasons or dates of planting.

Quantification of the time to flowering in chickpea germplasm has indicated that a wide range of flowering times exist (Singh et al., 1991; Pundir et al., 1988), similar to other closely related species such as lentil (Erskine et al., 1994). The involvement of several genetic systems responding to day length and temperature causes a typical

continuous frequency distribution of flowering time in chickpea (Kumar and Abbo, 2001). The chickpea crop is quantitatively long day in its response, but some relatively photoperiod insensitive genotypes are also available (Roberts et al., 1985).

A number of major loci controlling time to flowering have been reported in soybean (Cober et al., 1996) and pea (Weller et al., 1997). However, information on the genetic control of flowering time in chickpea is only beginning to accumulate. Kumar et al. (1985) reported that at least two different loci control flowering time in chickpea. Later, a major gene for flowering time with late flowering dominant over earliness was reported by Or et al. (1999) and Kumar and van Rheenen (2000). The presence of major gene opens the possibility for effective manipulation of the flowering time in chickpea for its adaptation to different environments. However, more research should be undertaken to identify other loci controlling flowering behavior in chickpea so that genotypes that meet specific growing environments can be developed.

Early flowering is beneficial for early maturity in many growing environments. Kumar and Rao (2001) provided evidence that the super-early flowering chickpea germplasm ICCV 96029 matured early as well. The flowering genes may influence maturity date through their effects on the onset of reproduction and duration of reproductive phase (Kumar and Abbo, 2001). Early flowering also helps to prolong the reproductive period, which is a major yield determinant (Bonfil and Pinthus, 1995). It appears that the early flowering character is beneficial for both early maturity and high grain yield. Early flowering and early podding genotypes would therefore aid in escaping end-of-season frost in western Canada. These characters should be considered as major objectives for chickpea improvement in this environment.

2.6.5 Agronomic considerations

Duration of crop maturity is a function of genotype, environment or their interaction, indicating that efforts to match crop duration to the length of the growing season could be partly met by adoption of appropriate agronomic practices. Increase in plant population density has advanced plant maturity, particularly in desi chickpea in the semi-arid environment in the Prairies (Gan et al., 2003). Interplant competition under dense population may lead to a more rapid depletion of the available soil moisture and nutrients, causing early transition to maturation phase. Early seeding will also have a direct effect on maturity in that it advances the timing of different phenological stages and subsequently maturity date. However, the cool spring weather in western Canada does not allow substantial advancement in sowing.

Management of soil mineral nutrition may, on the other hand, alter growth pattern and could have effects on maturity duration in chickpea and other crops. Preliminary studies by Gan et al. (2004) showed that application of nitrogen fertilizer significantly reduced days to maturity in chickpea in south-western Saskatchewan compared to non-fertilized checks or plots that received granular inoculant. In cotton, another indeterminate species, low potassium availability resulted in earlier termination of reproductive growth and a subsequent reduction in crop duration (Pettigrew, 2003). The prevailing assumption is that the crop runs out of potassium, causing an early termination of reproductive growth. However, this may also have a negative effect on yield. An improved understanding of plant nutrition in chickpea would help to better manage the crop for timely maturity and maximum grain yield.

3. Short Internode, Double Podding and Early Flowering Effects on Maturity and Other Agronomic Characters in Chickpea

Summary

Progress in chickpea breeding has been constrained by the lack of satisfactory genetic sources of early maturity in the short-season temperate environment of western Canada. It was hypothesized that the length of the chickpea lifecycle could be reduced through introgression of strategic genetic traits including short internode, double podding, and early flowering. Four populations E100Ym/CDC Anna, 272-2/CDC Anna, 298T-9/CDC Anna, and 298T-9/CDC Frontier were developed to test this hypothesis with the first parents of each cross being the donor of the short internode, double podding and early flowering traits, respectively. Also, the donor parents E100Ym, 272-2, and 298T-9 were intercrossed to pyramid the genes for these key traits. Segregating populations of F_2 to $F_{3:6}$ generations from biparental and gene pyramiding populations were then evaluated under greenhouse and field conditions. The result showed that genotypes with high expressivity of double podding (i.e. >15% of the podding nodes bearing double pods) were significantly earlier to mature than the single podding genotypes. For the early flowering populations, the earliest flowering lines were as early as the early flowering parent (298T-9) in both days to flowering and days to maturity. Days to flowering was positively associated with days to maturity ($r = 0.44$, $P < 0.001$), and partial path analysis revealed that days to flowering contributed to

days to maturity indirectly via days to first pod maturity. In the two early flowering populations 298T-9/CDC Anna and 298T-9/CDC Frontier, days to flowering determined about 32% of the variation in days to first pod maturity. However, the short internode trait had an undesirable effect in that all the short internode segregants were too late to mature. In conclusion, the alleles for double podding and early flowering may be used to improve earliness of crop maturity in chickpea and subsequently minimize the risks associated with the production of this crop in the Prairies.

3.1 Introduction

Chickpea has recently become an important pulse crop in western Canada, following pea *(Pisum sativum L.*) and lentil (*Lens culinaris* Medik). The improved cropping technologies of reduced summer fallow acreage, longer crop rotations and continuous cropping have all encouraged the expansion of pulse crops in the region (Saskatchewan Pulse Growers, 2000). Chickpea and other pulses are competitive compared to other crops in the rotation, providing a relatively high return over variable expenses in the semi-arid regions in western Canada (Saskatchewan Agriculture and Food, 2006b).

When a crop is placed in a new production area, some of the local production constraints are unique. Chickpea is a crop of Mediterranean origin and generally performs best with a long, warm growing season (Singh, 1997). In western Canada; however, the maturation phase of chickpea coincides with declining temperatures and wet conditions during the months of August through October, in sharp contrast to many

other growing environments. Since chickpea has a highly indeterminate growth habit, it continues to flower and set new pods under these conditions, resulting in delayed maturity and increased risk of frost damage.

Early maturity is a key agronomic trait for chickpea breeding in western Canada. Progress has been made in developing somewhat earlier maturing varieties, but even these often take longer to mature than the length of the growing season in the area. It was hypothesized that key genetic traits such as short internode, double podding and early flowering could be used as a strategy to accomplish this goal (Fig. 3.1). The effective coordinated action of the genes for these traits would, therefore, reduce requirement of a long growing season for chickpea and subsequently minimize production risk.

A spontaneous mutant E100Ym with distinct short internode phenotype and compact, dwarf plant type was reported in chickpea (Dahiya et al., 1984). Sandhu et al. (1990) observed monogenic inheritance for this trait, with the recessive gene *ptpt* ascribed to the mutant plant type. The main advantage of using a short internode trait in a breeding program is to reduce vegetative growth and increase the proportion of assimilate partitioned into grain. Short internode may subsequently lead to earlier crop maturity in environments such as western Canada where growing conditions often lead to excessive crop canopy development.

Chickpea typically produces a single pod per peduncle, but double podding genotypes bearing two pods per peduncle in some reproductive nodes are also available. Double podding is governed by a single recessive gene (ss) in chickpea and this trait confers a significant yield advantage under conditions in which the character is

Fig. 3.1. Key strategic genetic traits for early maturity in chickpea, short internode (top) and double podding (bottom).

sufficiently expressed (Sheldrake et al., 1978). Rubio et al. (2004) found that the double podding gene had no effect on yield, but contributed to higher yield stability. The effect of the double podding trait on yield stability might have stemmed from its involvement in earliness of crop maturity. Double podding may increase the total number of pod set, thus increasing the demand for assimilate and resulting in an earlier transition of main reproductive growth to physiological maturity.

Optimum time of flowering is a major component of crop environmental adaptation (Subbarao et al., 1995) and is a critically important trait for adaptation to specific latitudes (Bonato and Vello, 1999). According to Kumar and Abbo (2001), the flowering genes influence maturity through their effects on the onset of reproductive growth and then the subsequent duration of the reproductive phase. Time to flowering is a quantitative trait (i.e. controlled by several genes), but a major gene responsible for the majority of the variation in this trait has been reported (Or et al., 1999; Kumar and van Rheenen, 2000). The effect of these genes on maturity duration in the short-season temperate environment of western Canada remains to be quantified.

Favorable single genes have, in some instances, brought about major achievements in plant breeding; for example, dwarfing genes in wheat (Athwal, 1971), and genes for determinate/semi-determinate growth habit in soybean (Bernard, 1972). Poehlman and Sleper (1995) pointed out that most successes in plant breeding to date have originated from such favorable single genes. Taking this into account, a study was initiated to determine the effects of short internode, double podding, and early flowering alleles on earliness of crop maturity and other agronomic traits in chickpea in the short-season temperate environment of western Canada.

3.2 Materials and Methods

3.2.1 Biparental populations

Greenhouse experiment

Four single crosses were made as E100Ym/CDC Anna, 272-2/CDC Anna, 298T-9/CDC Anna, and 298T-9/CDC Frontier. The first parent in each cross had either short internode (E100Ym), double podding (272-2) or early flowering (298T-9) characteristics. CDC Anna (Vandenberg et al., 2003) and CDC Frontier (Warkentin et al., 2005b) are modern high-yielding cultivars developed for Saskatchewan and are from the desi and kabuli market classes, respectively. From each cross, 180 F_2 plants were evaluated under greenhouse conditions in summer 2003. Individual plants were grown in 20 cm pots filled with Redi-Earth soil (W.R. Grace and Co., ON, Canada). Photoperiod was set at 16/8 hour day/night regime and mean air temperature was 24 $\pm$ 3 ^{o}C. The plants were fertilized with fast release fertilizer (20N: 20P_2O_5: 20 K_2O) (CHISSO-ASAHI fertilizer Co. Ltd, Tokyo, Japan) at a rate of 5 g pot^{-1} one week after emergence and at 35 g pot^{-1} of controlled release type 100 (14N: 14P_2O_5: 14K_2O) (Plant Products Co. Ltd, ON, Canada) another week later. Plants were watered every 3─7 days depending on crop growth stage and corresponding water use. Data for days to flowering (number of days from seeding to appearance of first flower), days to first podding (number of days from seeding to appearance of first fully developed pod), days to first pod maturity (number of days from seeding to when the first pod turned brownish), percent pod maturity (percentage of matured pods at four months after seeding), number of nodes to first pod (number of nodes from the ground to the first pod on the main stem), height to first pod (height from ground to the bottom pod),

height at flowering (height of the plant at flowering), and plant height (height of the plant at physiological maturity) were recorded. Individual seed weight was determined as an average weight of ten well filled seeds. Pod filling duration was calculated as days to first pod maturity ─ days to first podding.

Field experiment

A single seed was taken from each F_2 plant above and grown in the same greenhouse to advance the generation. Then $F_{3:4}$ generation (i.e. F_4 families derived from individual F_3 plants) were grown in micro-plots at Saskatchewan Pulse Growers farm in summer 2004. Three rows micro-plot of 1m length and 0.3m row spacing was used for each genotype. These were laid out in augmented randomized complete block design (ARCBD) using the respective parental genotypes as repeated checks (Federer, 1956). Seeds were treated with a mixture of Apron FL (317 g L^{-1} metalaxyl) at a rate of 32 mL kg^{-1} seed and Crown (92 g L^{-1} carbathiin and 58 g L^{-1} thiabendazole) at a rate of 6 mL kg^{-1} seed to protect against seedling diseases. *Mesorhizobium ciceri* granular inoculant (Becker Underwood Inc., IW, USA) was applied in the seed rows at a rate of 5.6 kg ha^{-1}. Weeds were controlled using fall application of Pursuit (240 g L^{-1} imazethapyr) at a rate of 69 mL ha^{-1} plus Edge (5% ethalfluralin) at a rate of 28 kg ha^{-1}. The crop was protected against the fungal disease ascochyta blight using the fungicides Bravo 500 (500 g L^{-1} chlorothalonil) at a rate of 3.2 L ha^{-1} and Headline (250 g L^{-1} pyraclostrobin) at a rate of 395 mL ha^{-1}. Bravo 500 was applied at the time chickpea plants began flowering, followed 10 days later by Headline, then another 10 days later by a second application of Headline. Data on days to flowering, days to first pod

maturity, percent pod maturity, expressivity of double podding, and seed yield were collected. Expressivity of double podding was taken as the number of double podding nodes divided by the total number of podding nodes expressed as a percentage (Kumar et al., 2000).

From the $F_{3:4}$ families, three lines were selected from each cross for further testing. Selection was based on earliness to flower for the two early flowering populations, and expressivity of double podding for the double podding population. However, the short internode segregants from the respective cross were too late to mature and were not advanced. Instead, only the three earliest maturing lines were selected from the short internode cross. The selected lines (now $F_{3:5}$ generation) were grown under greenhouse conditions for seed multiplication to produce $F_{3:6}$ lines.

During summer 2005, the twelve selected $F_{3:6}$ lines (3 lines x 4 crosses) were grown along with the four parental lines 272-2, 298T-9, CDC Anna, and CDC Frontier and two early maturing check cultivars, CDC Cabri (Warkentin et al., 2005a) and Myles (Muehlbauer et al., 1998), at the Goodale farm near Saskatoon. Plots were arranged in a randomized complete block design (RCBD) with three replications. Plots were 4 m length with 3 rows each spaced 0.3 m apart. Seeds were treated with a mixture of Apron FL (317 g L^{-1} metalaxyl) at a rate of 32 mL kg^{-1} seed and Crown (92 g L^{-1} carbathiin and 58 g L^{-1} thiabendazole) at a rate of 6 mL kg^{-1} seed to protect against seedling diseases. Weed control was made with fall application of Pursuit (240 g L^{-1} imazethapyr) at a rate of 69 mL ha^{-1} plus Edge (5% ethalfluralin) at a rate of 28 kg ha^{-1} as well as a pre-seeding application of Centurion (240 g L^{-1} clethodim) at a rate of 198 mL ha^{-1}. The crop was protected against the fungal disease ascochyta blight using the

fungicides Bravo 500 (500 g L^{-1} chlorothalonil) at a rate of 3.2 L ha^{-1} and Headline (250 g L^{-1} pyraclostrobin) at a rate of 395 mL ha^{-1}. Bravo 500 was applied at the time chickpea plants began flowering, followed 10 days later by Headline, then another 10 days later by a second application of Headline. Data on days to maturity (days from seeding to when 90% of the pods turned brown), height at flowering, and plant height were recorded. Seed yield (kg ha^{-1}) and 100 seed weight (g) were determined after cleaning the seeds.

Data analysis

The segregation pattern for pod number per peduncle (double or single) and internode length (short or normal) were assessed in the F_2 of the respective cross. The t-test for unequal variances was used to compare single and double podding phenotypic classes for all the different phenological and agronomic characters measured. A regression approach was employed to assess the relationship of days to flowering with days to first podding and days to first pod maturity. For the 272-2/CDC Anna $F_{3:4}$ population grown in the field in 2004, days to first pod maturity, percent pod maturity and seed yield of the top 10% early lines and that for best double podding lines were compared with the population mean. Analysis of variance was carried out using SAS PROC GLM (SAS Institute Inc., 1999) on phenological and agronomic traits recorded for the $F_{3:6}$ genotypes grown in the field. Means were separated using Fisher's protected least significant differences (LSD) for P = 0.05.

3.2.2 Gene pyramiding population

Experimental set-up and data collection

A double cross (272-2/E100Ym//298T-9/E100Ym) was made among the short internode (E100Ym), double podding (272-2) and early flowering (298T-9) parents to pyramid the genes for these strategic genetic traits. From this cross, 180 F_2 plants were grown under greenhouse conditions in an ARCBD using CDC Anna and 272-2 as replicated checks (Federer, 1956) in summer 2004. Crop management practices including fertilization and watering were same as shown above for the biparental population. Data were collected on days to flowering, days to first pod maturity, percent pod maturity, 100 seed weight (g) and seed yield (g plant^{-1}).

From these, 128 $F_{2:3}$ families for which sufficient seed was available were grown in three-row micro-plots of 1 m length and 0.3 m row spacing at the Preston farm, Saskatoon in summer 2005. About 50 seeds were used in each micro-plot. The experiment was also laid out in the ARCBD using 272-2, 298T-9, CDC Anna, and CDC Cabri as replicated checks. Seeds were treated with a mixture of Apron FL (317 g L^{-1} metalaxyl) at a rate of 32 mL kg^{-1} seed plus Crown (92 g L^{-1} carbathiin and 58 g L^{-1} thiabendazole) at a rate of 6 mL kg^{-1} seed to protect against seedling diseases. Weed control was made with a pre-seeding application of Treflan (5% trifluralin) at a rate of 2.3 L ha^{-1}. For the field experiment, data were collected on days to flowering, days to first pod maturity, percent pod maturity, days to maturity, plant height, seed yield, and 100 seed weight as indicated above for the biparental populations.

Data analysis

Analysis of variance was carried out for both the greenhouse and field experiments using SAS PROC GLM (SAS Institute Inc., 1999) for the different phenological and agronomic characters as suggested by Scott and Milliken (1993). Pearson correlation coefficients among different phenological and agronomic traits were determined in the $F_{2:3}$ population. The direct and indirect effects of days to flowering on days to maturity were determined using a partial path coefficient analysis in the same $F_{2:3}$ family data (Williams et al., 1990; Bowley, 1999).

3.3 Results

3.3.1 Biparental populations

The segregation pattern for internode length and number of pods per peduncle did not deviate significantly from the 3:1 ratio expected for monogenic control (Table 3.1). The F_2 individuals from the short internode cross fell into two phenotypic classes, i.e., normal and short internode plants in the respective 3:1 ratio ($\chi^2 = 0.12$, $0.8 > P > 0.7$). The short internode allele also affected other plant characters. All individuals in this phenotypic class had dark green leaves, thick stems, and an erect, compact growth habit. Segregation for number of pods per peduncle also followed a single locus genetic model. The F_2 generation segregated into 3 single podding : 1 double podding phenotypic ratio ($\chi^2 = 0.74$, $0.4 > P > 0.3$). A more detailed genetic analysis revealed that time to flowering was controlled by two major genes plus polygenes in these populations (see Chapter Four), indicating the simple inheritance of this trait as well.

Data analysis demonstrated that short internode, double podding, and early flowering traits had separate effects on maturity characteristics in the respective F_2 population(s). The short internode allele had a negative effect on maturity. All the short internode segregants (43 in number, see Table 3.1) were too late such that pods rarely started to mature on these plants at four months after seeding, whereas the normal segregants had nearly reached full pod maturity at this time. Because of this delayed maturity, it was not practical to note maturity characteristics in the short internode plants or make detailed comparisons with the normal plants.

In this study, days to flowering was linearly and positively associated with each days to first pod maturity and days to first podding (Fig. 3.2). As expected, early flowering resulted in early initiation of pods and beginning of maturity of lower pods. In the two early flowering populations, 298T-9/CDC Anna and 298T-9/CDC Frontier, days to flowering determined about 32% of the variation in days to first pod maturity.

Double podding genotypes had a slightly higher mean number of pods per plant and attained higher percent pod maturity at four months after seeding compared to the single podding counterparts, but the differences were not statistically significant (Table 3.2). Also, no significant difference was noticed between single podding and double podding genotypes for all the other earliness traits assessed (Table 3.2). However, it should be noted that the expressivity of double podding was low and variable ranging from 0─34% under greenhouse conditions in the 272-2/CDC Anna population used for this study. In some cases, F_2 plants had two flowers per peduncle at some nodes, but only one pod fully developed resulting in zero expressivity of double podding. Unless it is expressed, double podding may not have a significant effect on earliness.

Table 3.1. Segregation for internode length and pod number per peduncle in two F_2 chickpea populations evaluated under greenhouse conditions.

Cross	*Segregation types*	*Number of plants*		χ^2	*P-value*
		Observed	Expected[z]		
E100Ym x CDC Anna (internode length)	Normal	137	135	0.12	0.7-0.8
	Short internode	43	45		
272-2 x CDC Anna (pod number per peduncle)	Single podded	140	135	0.74	0.3-0.4
	Double podded	40	45		

[z]number of segregants expected based on the single recessive gene hypothesis for short internode and double podding traits.

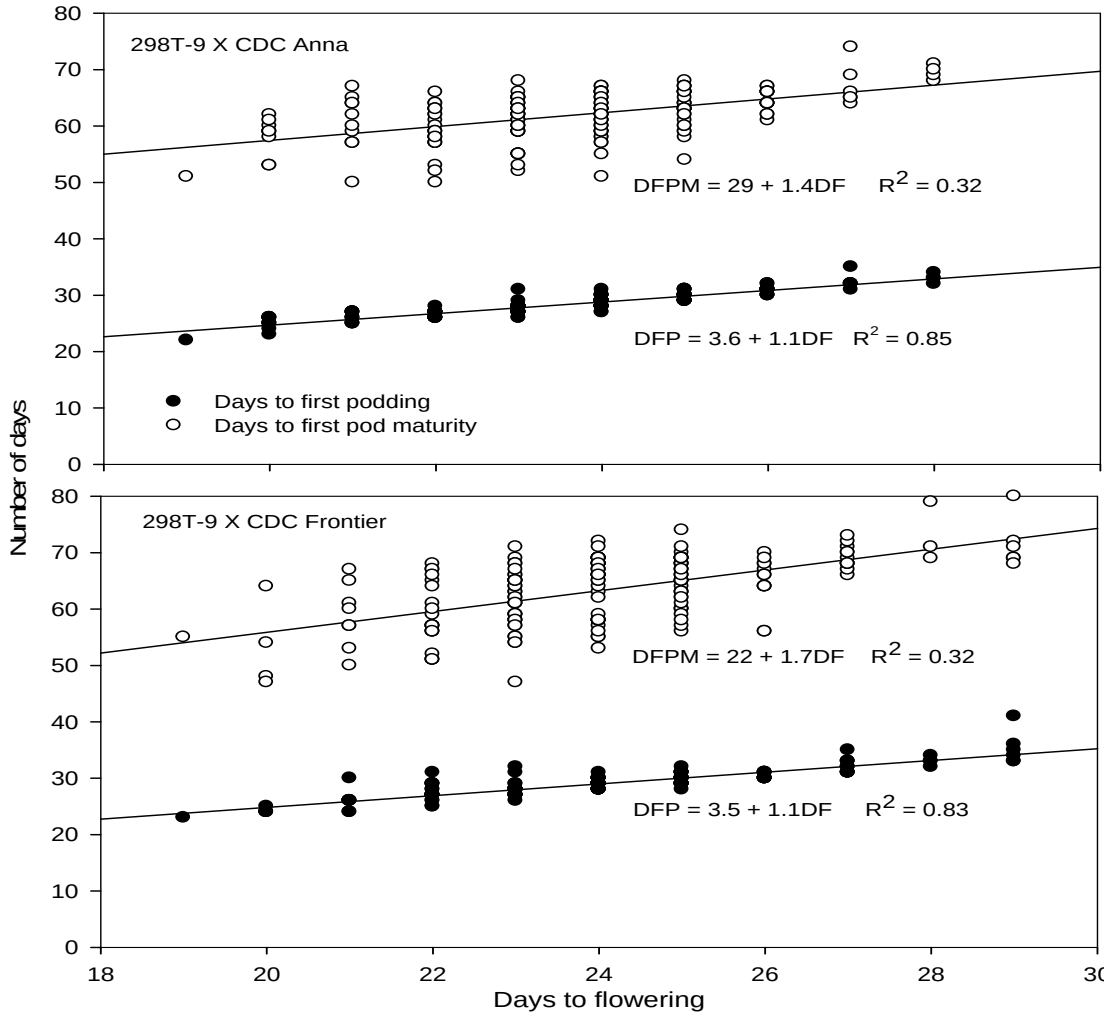

Fig. 3.2. Relationships of days to flowering (DF) with days to first podding (DFP) and days to first pod maturity (DFPM) in two F_2 populations of chickpea evaluated in the greenhouse.

Table 3.2. Comparison between single and double podding genotypes in some phenological and agronomic traits in 272-2/CDC Anna F_2 chickpea populations evaluated under greenhouse conditions.

Character	df	Phenotypic class		SE[z]	P-value[y]
		Single podding	Double podding		
Days to flowering	73	24	24	0.41	0.80
Days to first podding	74	29	29	0.47	0.84
Days to first pod maturity	75	60	60	0.88	0.53
Percentage pod maturity[x]	75	84	87	2.35	0.14
Number of nodes to first pod	75	14	14	0.45	0.21
Height to first pod (cm)	75	22	23	1.00	0.12
Height at flowering (cm)	74	27	26	1.14	0.78
Plant height (cm)	74	44	44	1.36	0.91
Pod filling duration (days)	74	32	31	0.72	0.37
Number of pods per plant	73	54	56	3.07	0.52
Mean individual seed weight (g)	75	0.26	0.26	0.06	0.78

[z] SE stands for standard error of differences between means.

[y] P values > 0.05 shows nonsignificant difference between the single podding and double podding phenotypic classes according to unequal variance t-test.

[x]Asessed at four months after seeding.

In agreement with the data from the F_2 populations evaluated in the greenhouse, the $F_{3:4}$ population from 272-2/CDC Anna showed wide variability for percent pod maturity at four months after seeding under field conditions in 2004 (Fig. 3.3). The 2004 season was generally cool and wet and crop maturity was delayed (Chapter 6, Table 6.1). Averaged over all individuals, percent pod maturity at four months after seeding was only 50.4%. The two parents 272-2 and CDC Anna had a mean of 30 and 68% of the pods matured at this time, respectively. However, few genotypes, essentially the double podding individuals, attained over 75% pod maturity. Mean percent pod maturity for genotypes that had higher expressivity of double podding was 81.3%, which is equivalent to the 80.7% mean percent pod maturity for top 10% early genotypes (Table 3.3). Genotypes with higher expressivity of double podding also had significantly higher grain yield than the mean of the population. These results reveal that double podding hastened progress towards maturity and increased yield in genetic backgrounds where the character was sufficiently expressed.

Field comparison of the best $F_{3:6}$ genotypes revealed highly significant differences among these genotypes in phenological and other agronomic characters (Table 3.4; Fig. 3.4). The test genotypes were selections from the short internode, double podding, and early flowering crosses based on their superiority in the expression of the respective trait (see Materials and Methods). The three genotypes selected from the double podding population (Y9421-026, Y9463-028 and Y4912-039) were at least one week earlier maturing than the parents and other check varieties. The mean expressivity of double podding was 32% for Y9421-026, 34% for Y9463-028, and 16% for Y4912-039 as compared to the 10% mean expressivity of double podding for the

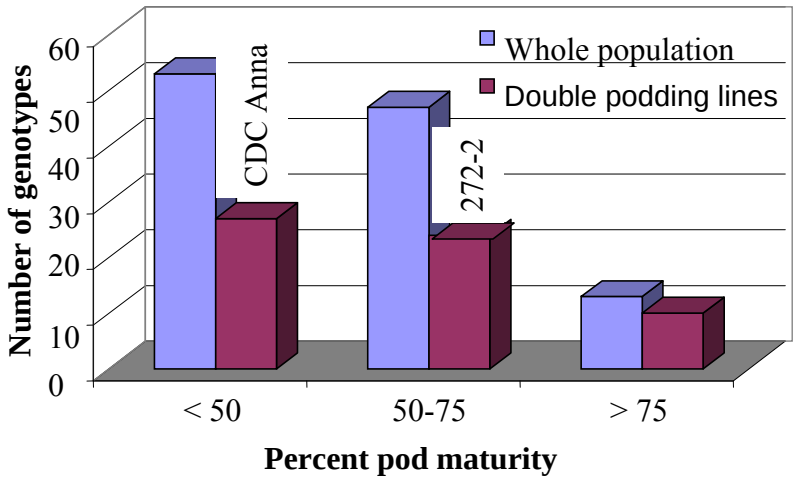

Fig. 3.3. Distribution of percent pod maturity at four months after seeding in $F_{3:4}$ 272-2/CDC Anna population of chickpea evaluated at Saskatchewan Pulse Growers farm near Saskatoon in 2004.

Table 3.3. Mean ($\bar{x}$) and standard error (*SE*) of earliness traits and grain yield in $F_{3:4}$ 272-2/CDC Anna population evaluated at Saskatchewan Pulse Growers farm in 2004.

Variable		*Population mean*	*All double podding lines*	*Best double podding lines*[z]	*Top 10% early lines*
Population size (N)		115	60	7	11
Days to first pod	$\bar{x}$	90	88	79	80
maturity	*SE*	0.81	1.09	0.72	0.59
Percent pod	$\bar{x}$	50.4	51.3	81.3	80.7
maturity[y]	*SE*	2.32	3.40	0.36	0.47
Seed yield	$\bar{x}$	2274	2246	2981	2724
(kg ha^{-1})	*SE*	57.3	76.7	299.5	231

[z] Lines that were rated high for expressivity of double podding.

[y]Assessed at four months after seeding.

Table 3.4. Mean seed yield and some phenological and agronomic characters in the best $F_{3:6}$ chickpea genotypes selected from short internode, double podding and early flowering populations compared to their parents and other check varieties at the Goodale farm near Saskatoon in 2005.

Category	*Genotype*	*Days to maturity*	*Height at flowering (cm)*	*Plant height (cm)*	*Seed yield (kg ha^{-1})*	*100 seed weight (g)*
Short internode	Y3842-005	146	40	68	3387	19.6
(E100Ym/CDC	Y3842-023	149	38	68	2729	15.2
Anna)	Y3861-041	139	40	60	3117	19.5
Double podding	Y9421-026	129	38	52	3020	16.8
(272-2/CDC	Y9463-028	132	42	51	2896	13.2
Anna)	Y4912-039	134	39	56	2773	15.1
Early flowering	Y6161-009	138	40	54	3722	18.2
(298T-9/CDC	Y6172-011	142	39	57	3435	17.8
Anna)	Y1611-040	149	39	70	2340	15.6
Early flowering	Y7211-039	148	39	61	2015	21.8
(298T-9/CDC	Y2721-065	147	37	67	2491	20.8
Frontier)	Y2721-089	145	36	65	2779	20.2
Parental	272-2	142	34	54	2706	13.4
genotypes	298T-9	149	37	65	2256	18.6
	CDC Anna	153	41	80	1364	19.9
	CDC Frontier	151	46	62	2342	35.9
Check varieties	CDC Cabri	145	45	69	3277	29.2
	Myles	145	41	69	2132	18.8
CV (%)		3.6	8.4	12.1	16.2	3.8
$LSD_{0.05}$		9.2	5.5	12.6	1156	4.4

Fig. 3.4. Progress towards maturity in double podding genotype Y9421-026 (center) as compared to single podding genotypes at Goodale farm near Saskatoon in 2005.

double podding parent 272-2. The double podding genotypes in this experiment had a relatively small increase in height between flowering and maturity stages. The differences between height at flowering and plant height were 10─15 cm in the double podding lines compared to >20 cm in CDC Anna, 298T-9, CDC Cabri, and Myles.

3.3.2 Gene pyramiding population

Analysis of variance revealed significant differences among the F_2 genotypes of the gene pyramiding population evaluated in greenhouse for days to first pod maturity and 100 seed weight, whereas genotypic differences for percent pod maturity and seed yield were not significant (Table 3.5). Also, there were significant genotypic differences among the $F_{2:3}$ genotypes of this population evaluated in the field in phenological traits, 100 seed weight, and seed yield (Table 3.5).

In the same $F_{2:3}$ population evaluated in the field, days to flowering was positively associated with days to first pod maturity, days to maturity, plant height, and 100 seed weight (Table 3.6). As expected, the association between days to flowering and percent pod maturity was negative. Also, the Pearson correlation analysis showed that days to flowering and maturity were positively associated with 100 seed weight, indicating that early flowering and maturity may imply reduced seed weight in some genetic backgrounds. Partial path analysis revealed that the effect of days to flowering on days to maturity was mainly indirect through days to first pod maturity (Table 3.7). The indirect contribution of days to flowering on days to maturity via days to first pod maturity was 0.3 as compared to 0.1 for the direct effect. The effects of days to flowering on days to maturity via plant height and 100 seed weight were low.

Table 3.5. Analysis of variance for seed yield, 100 seed weight and some phenological traits in a chickpea population derived from intercrosses among short internode, double podding and early flowering parents and assessed under greenhouse and field conditions.

		Mean squares				
Source of variation	*df*	Days to first pod maturity	Percent pod maturity	Days to maturity	100 seed weight (g)	Seed yield (kg ha^{-1})
Greenhouse (F_2 generation)						
Replication	9	13.6	122.5	NR	10.3	34.5
Checks	2	237.6**	987.8	NR	756.5**	559.7
Test entries (checks)	142	19.6*	106.4	NR	19.6**	56.3
Error	9	7.3	348.9	NR	1.8	96.2
Field ($F_{2:3}$ generation)						
Replication	3	15.1	15.6	15.7	1.7	116644
Checks	4	83.7**	111.3**	197.4**	270.6**	528903
Test entries (checks)	125	90.7**	98.8**	48.3**	22.1**	618228*
Error	9	4.2	11.8	8.2	1.3	159635

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

NR – not recorded.

Table 3.6. Pearson correlation coefficients among some phenological and agronomic traits in $F_{2:3}$ population of chickpea (N = 126) from intercrosses among short internode, double podding and early flowering parents and evaluated at Preston farm, Saskatoon in 2005.

Character	*DFPM*	*PPM*	*DM*	*PTHT*	*100 SW*
Days to flowering (DF)	0.46**	-0.50**	0.44**	0.43**	0.24**
Days to first pod maturity (DFPM)	-	-0.78**	0.73**	0.35**	0.26**
Percentage pod maturity (PPM)		-	-0.82**	-0.36**	-0.18*
Days to maturity (DM)			-	0.38**	0.22*
Plant height (PTHT) (cm)				-	0.36**

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

100 SW – 100 seed weight.

Table 3.7. Partial path analysis for the direct and indirect effects of days to flowering on days to maturity in $F_{2:3}$ population of chickpea (N = 126) from intercrosses among short internode, double podding, and early flowering parents and evaluated at Preston farm, Saskatoon in 2005.

Type of effect	*Coefficient*
Direct effect	0.10
Indirect effect via days to first pod maturity	0.30
Indirect effect via plant height (cm)	0.05
Indirect effect via 100 seed weight (g)	- 0.01
Total (= r)	0.44
R^2	0.58

3.4 Discussion

Accumulation of favorable alleles of important morphological and phenological traits through breeding may help to develop more growth efficient plant types with hastened progress towards maturity. This might be a feasible breeding strategy for chickpea in environments such as western Canada where progress in development of early maturing germplasm is constrained by the lack of satisfactory genetic sources of early maturity. With this consideration, the effects of three strategic genetic traits, i.e., short internode, double podding, and early flowering as part of an overall strategy of reducing the chickpea's seasonal length requirement in western Canada were analyzed.

The present study revealed that the short internode allele had an undesirable effect in that all the short internode segregants were extremely late to mature. This was probably due to the pleiotropic action of the locus as previously reported by Sandhu et al. (1990). The short internode allele is likely involved in gibberellin metabolism, which affected other characters such as leaf size and color, flowering, and pod development and then crop maturity. In pea, the gibberellin mutant alleles *le, lh, ls,* and *na* have a range of minor effects including reduction in leaf size and a darkening in leaf color together with reduction in internode length (Reid, 1986; Reid and Ross, 1993), the latter which characteristically matches the phenotype of the short internode segregants in the E100Ym/CDC Anna population used for this study. However, the short internode trait from a different allele may still be useful to induce early maturity in chickpea. At least two other dwarf mutants have been reported in chickpea (Singh and Dahiya, 1974; Shamsuzzaman et al., 2002). Short internode could help to reduce excessive canopy development, which is a main factor delaying chickpea maturity in

wet seasons in the western Canada. In crops such as wheat and rice, dwarfing genes have been used to increase lodging resistance and harvest index and to contribute to early maturity (Athwal, 1971). Also, a more compact canopy would allow an increase in population density and provide an opportunity to maximize grain yield.

Short plant stature resulting from short internodes may not be amenable to mechanized harvesting. But the interaction of different internode length alleles with each other and with the polygenic background for plant height should allow ranges of plant height as observed in pea (Reid, 1986) and lentil (Ladizinsky, 1997). This should enable development of chickpea varieties with reduced internode length but tall enough in height for combine harvesting.

The results of this study demonstrated that double podding trait had a significant effect on days to maturity. For the $F_{3:4}$ double podding population evaluated in the field in 2004, the earliest materials were essentially the double podding genotypes (Fig. 3.3). In this test, genotypes with high expressivity of double podding had a mean of 81.3% pods mature at four months after seeding as compared to the 50.4% overall mean percent pod maturity (Table 3.3). Further, the three $F_{3:6}$ genotypes selected from the double podding population for superior expressivity of this trait were significantly earlier to mature than the other genotypes and check varieties included in the field test in 2005 (Table 3.4; Fig. 3.4). However, when comparison was made based on simple presence or absence of double podding irrespective of its expressivity as in the F_2 of the biparental population, the advantage of double podding over single podding in earliness of crop maturity was not significant (Tables 3.2). This finding implies that double podding is beneficial for earliness of crop maturity in genetic backgrounds that allow

higher expressivity of this trait. Rubio et al. (2004) reported that the double podding allele conferred greater yield stability than the single podding allele in the Mediterranean region. The effect of double podding on yield stability is probably due to its positive contribution to early maturity. The presence of two pods per peduncle instead of one produces a large sink more rapidly and places an increased demand for photosynthate on the crop, hastening the switch from vegetative to grain filling mode. This hypothesis was supported by the evidence that double podding genotypes had a relatively small increase in height between flowering and maturity.

Kumar et al. (2000) reported that double podding plants produced slightly smaller seed size than their respective single podding segregants, but no statistical test substantiating this was presented. In this study there was no difference between the single and double podding phenotypic classes in seed size. The correlation between expressivity of double podding and seed size was not significant either ($r = 0.28$; $p = 0.72$). Rubio et al. (2004) also reported that double podding had no effect on seed size, implying that the double podding trait can be incorporated into small as well as large seeded genetic backgrounds. However, further study using different genetic backgrounds and ranges of seed sizes is required to reach at a strong conclusion about the relationship of double podding with seed size in chickpea.

In agreement with the reports of Kumar et al. (2000) the expressivity of double podding was consistently higher in some genotypes than others in our population. High expression of double podding brings about an increase in seed yield in addition to possible contributions to early maturity (Kumar et al., 2000). Therefore, favorable

genetic backgrounds for high expressivity of double podding need to be determined in chickpea so that the benefits of this trait may be maximized.

The significance of early flowering in reducing duration of crop maturity has been well recognized particularly in semi-arid (Subbarao et al., 1995; Kumar and Abbo, 2001) and Mediterranean regions (Rubio et al., 2004). In these environments, early flowering enables the crop to advance in reproductive growth before evaporative demand and high temperature stress become critical (Kumar and Abbo, 2001). Our study showed that time to flowering influenced maturity duration in chickpea mainly through its effect on timing of the beginning of maturity of lower pods in the short-season temperate environment of western Canada. Time to flowering was positively associated with days to maturity, but partial path analysis clearly showed that the relation of days to flowering with days to maturity was indirect mainly via days to first pod maturity. Early commencement of maturity of lower pods would be beneficial to progress towards full crop maturity before the occurrence of fall frost, and should reduce the risk of frost damage to chickpea crops in western Canada.

Significant differences were noticed within the segregating populations in time to flowering. About ten days difference was noticed between the earliest and latest flowering genotypes in both the biparental and gene pyramiding populations. Inheritance studies showed that time to flowering is determined by two major genes plus polygenes in these populations (Anbessa et al., 2006), and these genes can be easily incorporated into modern high-yielding genotypes. A further reduction in time to flowering may be achieved by the introduction of allelic variation for day length and

temperature responses derived from alien germplasm sources such that an extra early flowering and maturity habit enable the crop to escape frost damage.

Time to flowering was positively associated with 100 seed weight, which is in contrast to the general assumption that a long grain-filling period results in greater seed size. Hovav et al. (2003) also observed a significant and positive genetic correlation between days to flowering and mean seed weight. It appears that the genes which control time to flowering also pleiotropically affect other traits such as seed size as observed in soybean by Ellis et al. (2000). There was also a positive association between time to flowering and plant height in our study. The nature of this association seems physiological in that late flowering genotypes have more time for vegetative growth and grow taller.

In conclusion, both the double podding and early flowering traits had significant beneficial effects by reducing crop duration in chickpea in the short-season temperate environment of western Canada. Pyramiding double podding, early flowering, and other strategic genetic traits should lead to the development of extra short duration chickpea genotypes more suited for cultivation in the Prairies and similar environments. In the Prairies, early maturity is associated with high and stable yield and superior quality for the market. Although this study disproved the hypothesis that earliness could also be induced through short internode in chickpea, further studies are required using different alleles for this trait before a conclusion can be drawn.

4. Inheritance of Time to Flowering in Chickpea in a Short-season Temperate Environment

Summary

Time to flowering, measured as the number of days from seeding to flowering, is central in determining the adaptation and productivity of chickpea in many growing environments. We studied the genetic control of this trait in three crosses: 272-2/CDC Anna, 298T-9/CDC Anna and 298T-9/CDC Frontier. From each cross, 180 F_2 plants and parents were evaluated for time to flowering under greenhouse conditions. In summer 2004, multiple generations including P_1, F_1, P_2, F_2 and $F_{2:3}$ (also called MG5) were evaluated for time to flowering under field conditions. The data on time to flowering in the F_2 populations were continuous in distribution, but deviated from a normal distribution. The $F_{2:3}$ families derived from this showed a bimodal distribution for time to flowering, a typical case of major gene inheritance model. A joint segregation analysis (JSA) of MG5 revealed that time to flowering in chickpea was controlled by two major genes along with other polygenes. Late flowering was dominant over early flowering for both major genes with digenic interaction between them, mainly an additive x additive type. This information can be used to formulate the most efficient breeding strategy for improvement of time to flowering in chickpea in the short-season temperate environment of western Canada.

4.1 Introduction

Chickpea crops often experience short growing seasons as a result of drought, heat or end-of-season frost (Khanna-Chopra and Sinha, 1987). Early flowering is a key factor in formation and maturation of pods before the occurrence of those abiotic stresses. Kumar and Abbo (2001) acknowledged that time to flowering plays a central role in determining the adaptation and productivity of this crop in short growing environments.

The flowering time of chickpea is variable depending upon season, sowing date, latitude, and altitude (Summerfield and Roberts, 1988). According to Roberts et al. (1985), time to flowering was a function of temperature and photoperiod in chickpea. Ellis et al. (1994) further noticed that in some chickpea genotypes, time to flowering was influenced by photoperiod and temperature, while in others flowering time was determined solely by photoperiod.

Gumber and Sarvjeet (1996) studied the genetics of time to flowering in three crosses of chickpea and found that it was controlled by two genes. Kumar and van Rheenen (2000) observed a bimodal distribution for time to flowering in chickpea and deduced the presence of one major gene (*Efl-1/efl*-1) plus polygenes for this trait. Or et al. (1999) also supported this result, but they associated the major gene with sensitivity to photoperiod (*Ppd/ppd*). Kumar and Abbo (2001) suggested that the major early flowering alleles *efl-1* and *ppd* may be located at the same locus, although no experimental evidence supporting this hypothesis is yet available. Analysis of quantitative data by Cho et al. (2002) revealed a quantitative trait locus (QTL) for days

to flowering. But, the distinction between a major gene and a QTL is sometimes rather artificial, because once a QTL is identified and located it effectively becomes a major gene (Knott et al., 1991).

The genetics of time to flowering needs to be sufficiently understood in order to fine-tune genotypes to the demands of a particular environment. The ability to efficiently manipulate time to flowering is a crucial component of chickpea improvement (Kumar and Abbo, 2001). The above evidence indicates that genetic variation for time to flowering is mediated by genes of variable, rather than equal, effects. If a major gene with a significant effect on the variation can be identified, this can be manipulated in a directed fashion. However, co-segregating polygenes and environmental effects make the detection of major genes difficult.

Joint segregation analysis (JSA) was applied for the analysis of major-gene and polygenes mixed quantitative variation in plants in recent years (Wang and Gai, 2001). It has been used to analyze mixed inheritance models in human and animal populations over the last four decades (Elston and Steward, 1973; Knott et al., 1991). In brief, the method works as follows: first, some possible genetic models are hypothesized and likelihood functions are established for the different genetic models. Then maximum likelihood estimates of the parameters contained in each genetic model are obtained. The best fitting genetic model is selected based on Akakie's information criterion (Akakie, 1977 cf Knott et al., 1991). The objective of this study was to determine the most appropriate genetic model describing the variation in time to flowering in chickpea in a short-season temperate environment of western Canada.

4.2 Materials and Methods

4.2.1 Populations and experimental set-up

Three crosses 272-2/CDC Anna, 298T-9/CDC Anna and 298T-9/CDC Frontier were made at the University of Saskatchewan, Saskatoon, Canada. Genotypes 272-2 and 298T-9 were selected from field nurseries as early flowering lines (Table 4.1). They both had ICCV 96029 as one of their parents, which was reported as the world's earliest flowering chickpea germplasm to date (Kumar and Rao, 2001). Based on ratings in Saskatchewan, CDC Anna and CDC Frontier are late flowering genotypes of desi and kabuli market classes, respectively. The F_1 was advanced to F_2 and 180 F_2 plants from each cross were evaluated in the greenhouse in summer 2003. A single seed was taken from each F_2 plant to produce F_3 plants in the same greenhouse during fall 2003/winter 2004. In both cases one plant was grown in each 20 cm diameter pot filled with Redi-Earth soil (WR Grace and Company, Ajax, ON, Canada). Photoperiod was maintained at 18 hours and mean air temperature was 24 ± 3 ^{o}C in the greenhouse. During summer 2004, all the P_1, F_1, P_2, F_2 and $F_{2:3}$ populations from saved seed at each generation were evaluated in a field experiment at Saskatchewan Pulse Growers farm near Saskatoon (latitude 52^{o}09'N, longitude 106^{o}36'W). The maximum day length at this location was about 18 hours. Fifteen space-planted individual plants were used for each P_1, F_1 and P_2, whereas the F_2 individuals ranged from 121—143 per cross. The $F_{2:3}$ generation had 115 families of about 30 plants each in all the three crosses. Weed control was made with fall application of Pursuit (240 g L^{-1} imazethapyr) at a rate of 69 mL ha^{-1} plus Edge (5% ethalfluralin) at a rate of 28 kg ha^{-1} . The crop was protected against the fungal disease ascochyta blight using the fungicides Bravo 500 (500 g L^{-1}

chlorothalonil) at a rate of 3.2 L ha^{-1} and Headline (250 g L^{-1} pyraclostrobin) at a rate of 395 mL ha^{-1}. Bravo 500 was applied at the time chickpea plants began flowering, followed 10 days later by Headline, then another 10 days later by a second application of Headline. Time to flowering, i.e., the number of days from seeding to flowering, was recorded. The distribution patterns of time to flowering data for F_2 populations and their $F_{2:3}$ progeny were analyzed.

4.2.2 Joint segregation analysis

Genetic models

Five classes of genetic models were considered to select the one that best explains the variation in time to flowering in chickpea (Table 4.2). Taking into account gene action (additive, dominance, additive-dominance or additive-dominance-epistasis), we further set up model types within each class and overall 26 scenarios were considered.

Table 4.1. Days to flowering for parental genotypes under short and long photoperiod regimes as assessed under growth chamber conditions[z].

	Photoperiod	
Genotype	18 hour	12 hour
298T-9	25	38
272-2	25	37
CDC Anna	28	44
CDC Frontier	30	51
LSD $_{(0.05)}$	2.9	2.8
CV (%)	5.4	3.3

[z] Five plants per pot evaluated in three replications.

Table 4.2. Genetic models in the joint segregation analysis of the five generations of P_1, F_1, P_2, F_2 and $F_{2:3}$ (based on Zhang et al., 2003).

Class	Major-gene	Polygenes	Model type	
			Only major gene	Mixed major gene & polygenes
Polygenes	-	Additive-dominant [d][h]	-	C-1
	-	Additive-dominant-epistasis [d][h][i][j][l]	-	C-2
One major gene	Additive-dominant d, h	Additive-dominant-epistasis [d][h][i][j][l]	A-1	D
	Additive-dominant d, h	Additive-dominant [d][h]	A-1	D-1
	Additive d (h=0)	Additive-dominant [d][h]	A-2	D-2
	Completely dominant h(h=d)	Additive-dominant [d][h]	A-3	D-3
	Completely negative dominant h (-h=d)	Additive-dominant [d][h]	A-4	D-4
Two major genes	Additive-dominant-epistasis $d_1, d_2, h_1, h_2, i, j_{12}, j_{21}, l$	Additive-dominant-epistasis [d][h][i][j][l]	B-1	E
	Additive-dominant-epistasis $d_1, d_2, h_1, h_2, i, j_{12}, j_{21}, l$	Additive-dominant [d][h]	B-1	E-1
	Additive-dominant $d_1, d_2, h_1, h_2, i = j_{12} = j_{21} = l = 0$	Additive-dominant [d][h]	B-2	E-2
	Additive $d_1, d_2, h_1 = h_2 = 0$	Additive-dominant [d][h]	B-3	E-3
	Equally additive d ($=d_1 = d_2, h_1 = h_2 = 0$)	Additive-dominant [d][h]	B-4	E-4
	Completely dominant ($d_1 = h_1, d_2 = h_2$)	Additive-dominant [d][h]	B-5	E-5
	Equally dominant $d_1 = h_1 = d_2 = h_2$	Additive-dominant [d][h]	B-6	E-6

d, h - additive and dominance effects of major gene for model A and D; d_1, h_1 - additive and dominance effects of the first major gene for model B and E; d_2, h_2 – additive and dominance effects of the second major gene for model B and E; i, j_{12}, j_{21}, and l – additive x additive, additive x dominance, dominance x additive, dominance x dominance epistatic effects between the two major genes; [d],[h],[i][j][l] – additive effects, dominance effects, additive x dominance (or dominance x additive) and dominance x dominance epistatic effects of the polygenes.

Estimation of component parameters

The maximum likelihood estimates of the component parameters in each genetic model were obtained by the expectation and iterated maximization algorithm (Zhang et al., 2003). Suppose a quantitative trait is controlled by one major gene AA and polygenes. The F_1 from a cross between high and low parents would be Aa for the major gene. Three genotypes are possible at F_2 with segregation ratio of 1:2:1. The $F_{2:3}$ populations will have the same mixture of genotypes as F_2, but the proportion of individuals will change. Because of the effect of polygenes and environmental variance, for any given major genotype, the phenotypes of all individuals are independently and normally distributed and therefore the distribution of MG5 would be:

$$P_1: X_{1i} \sim N(\mu_1, \sigma^2); F_1: X_{2i} \sim N(\mu_2, \sigma^2); P_2: X_{3i} \sim N(\mu_3, \sigma^2)$$

$$F_2: X_{4i} \sim (1/4)\, N(\mu_{41}, \sigma^2_{41}) + (1/2) N(\mu_{42}, \sigma^2_{42}) + (1/4)\, N(\mu_{43}, \sigma^2_{43})$$

$$F_{2:3}: X_{5i} \sim (1/4)\, N(\mu_{51}, \sigma^2_{51}) + (1/2) N(\mu_{52}, \sigma^2_{52}) + (1/4)\, N(\mu_{53}, \sigma^2_{53})$$

P_1, F_1 and P_2 are assumed to have equal variance (σ^2) and with their respective means of μ_1, μ_2, μ_3; $\mu_{41}, \mu_{42}, \mu_{43}$ are means of the three major F_2 genotypes AA, Aa and aa, respectively; $\sigma^2_{41} = \sigma^2_{42} = \sigma^2_{43} = \sigma^2_4$ (common variance of components in F_2); $\mu_{51}, \mu_{52}, \mu_{53}$ represents means of $F_{2:3}$ families derived from AA, Aa and aa, respectively; σ^2_{52} is the variance of the component having mean μ_{52} and σ^2_{51} and σ^2_{53} are the common variance of the non-segregating $F_{2:3}$ families for the locus. Accordingly the component parameters estimated include $\mu_1, \mu_2, \mu_3, \mu_{41}, \mu_{42}, \mu_{43}, \mu_{51}, \mu_{52}, \mu_{53}, \sigma^2, \sigma^2_4, \sigma^2_{51}, \sigma^2_{52}$, and σ^2_{53}.

Model selection

To allow for different hypotheses depending on different numbers of unknown parameters, the hypothesis that maximizes the expected entropy is chosen (Akakie, 1977 cf Knott et al., 1991). For this purpose, we chose the hypothesis that leads to the smallest Akakie's information criterion (AIC) as the best fitting:

AIC = (-2) $\log_e$(maximum likelihood) + 2 (number of independently estimated parameters)

Estimation of genetic parameters

Once the component parameters are set it is possible to derive genetic parameters from them. Considering the above example again we obtain the following relationships for major-gene and polygenes mixed inheritance:

$\mu_1 = m + d + [d] + [i]$ $\mu_{41} = m + d + (1/2)[h] + (1/4)[l]$ $\mu_{51} = m + d + (1/4)[h] + (1/16)[l]$

$\mu_2 = m + h + [h] + [l]$ $\mu_{42} = m + h + (1/2)[h] + (1/4)[l]$ $\mu_{52} = m + h + (1/4)[h] + (1/16)[l]$

$\mu_3 = m - d - [d] + [i]$ $\mu_{43} = m - d + (1/2)[h] + (1/4)[l]$ $\mu_{53} = m - d + (1/4)[h] + (1/16)[l]$

m is a notation for overall population mean and the remaining are as described in Table 4.2.

Variances were partitioned into components based on the following relationships:

1) $\sigma^2_4 = \sigma^2_{40} + \sigma^2$ where σ^2_4 is the common variance across all F_2 genotypes, σ^2_{40} is the polygenic variance in F_2 population, σ^2 is the environmental variance.

2) $\sigma^2_{5t} = \sigma^2_{50} + \sigma^2/n + V_{mg}$ where σ^2_{50} and V_{mg} are variances due to polygenes and major gene in $F_{2:3}$ population, respectively and n is the number of plants observed.

$V_{mg1} = V_{mg3} = 0$, $V_{mg2} = ½\ d^2 + 1/4h^2$

4.3 Results

4.3.1 Frequency distribution of time to flowering

The F_2 populations evaluated in the greenhouse showed continuous variation for time to flowering (Fig. 4.1). The majority of the individuals fell between the two parents for time to flowering, but a few were one to two days earlier than the early parent and others were up to three days later than the respective late parent. The data on time to flowering in this F_2 population deviated from normal distribution for all three crosses ($P < 0.05$), as revealed by the Shapiro-Wilk test of the SAS PROC UNIVARIATE (SAS Institute Inc., 1999). The distribution of time to flowering data in these F_2 populations was skewed towards the late parental type (Fig. 4.1).

When F_2 was advanced to F_3, some genotypes derived from the late flowering F_2 plants flowered earlier than the population mean at F_3, while a few others which were early at F_2 flowered later than the population mean at F_3 (Fig. 4.2). Late flowering is dominant over earliness in chickpea (Or et al., 1999; Kumar and van Rheenen, 2000), and F_2 genotypes which were late to flower could be early at F_3 because of segregation in the heterozygous plants. The opposite move from early in F_2 to late in F_3 would probably indicate the involvement of epistatic gene action. The early and late parents included as checks were earlier and later than the population mean in time to flowering across both tests, respectively.

Summer 2004 was cooler than average at Saskatoon (Chapter 6, Table 6.1). As a result crop growth was slow and flowering was delayed for chickpea. Under these conditions, the early parents flowered in 52─53 days from seeding whereas the late parents took 60─61 days (Fig. 4.3). The distributions of time to flowering data for the

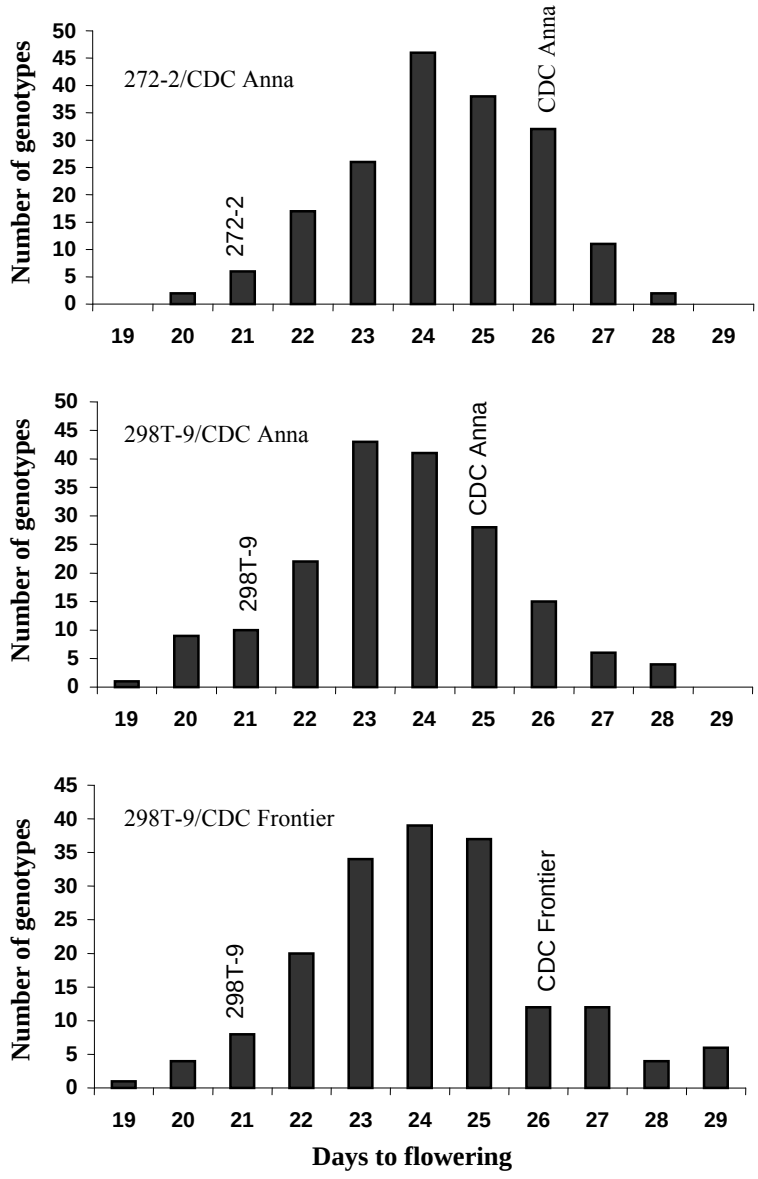

Fig. 4.1. Frequency distribution of days to flowering in three F_2 populations of chickpea evaluated in greenhouse**.**

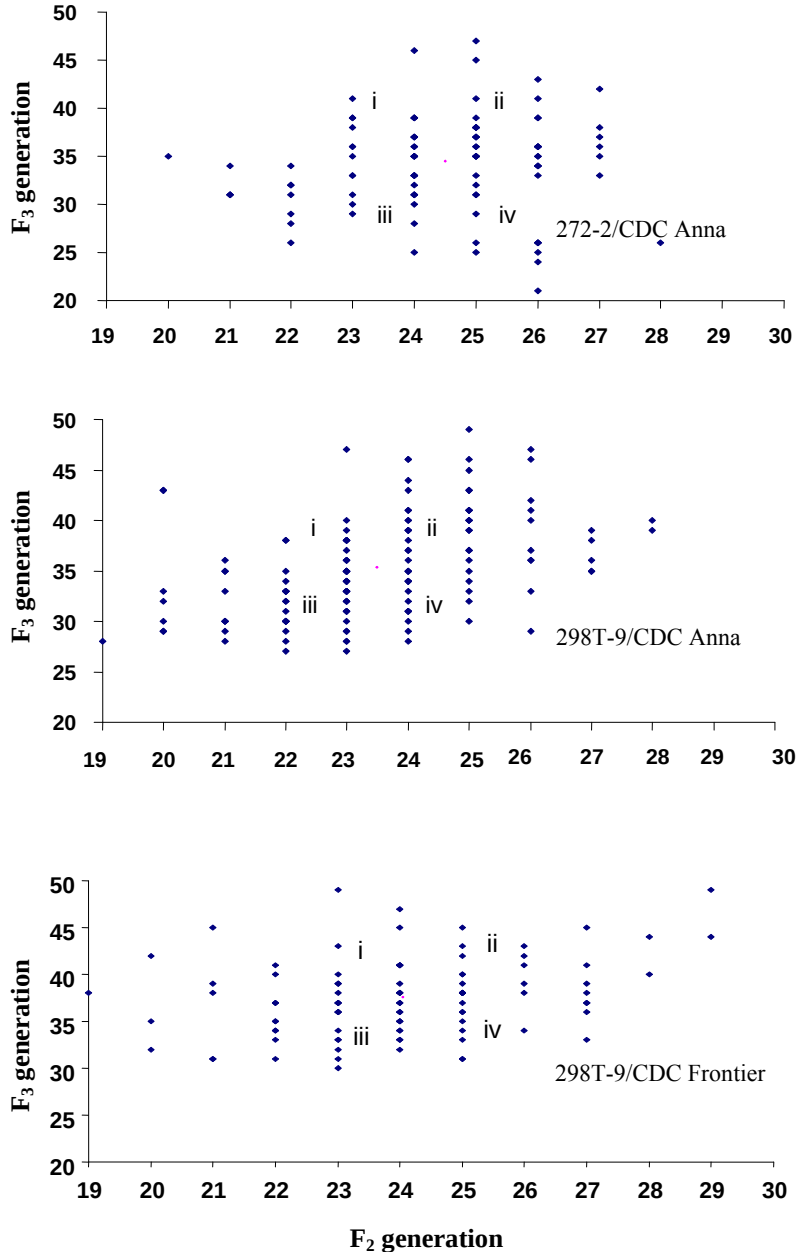

Fig. 4.2. Days to flowering at F_2 and F_3 generations in three crosses of chickpea evaluated in greenhouse i) early at F_2 but late at F_3 ii) late at both F_2 and F_3 iii) early at both F_2 and F_3 iv) late at F_2 but early at F_3 .

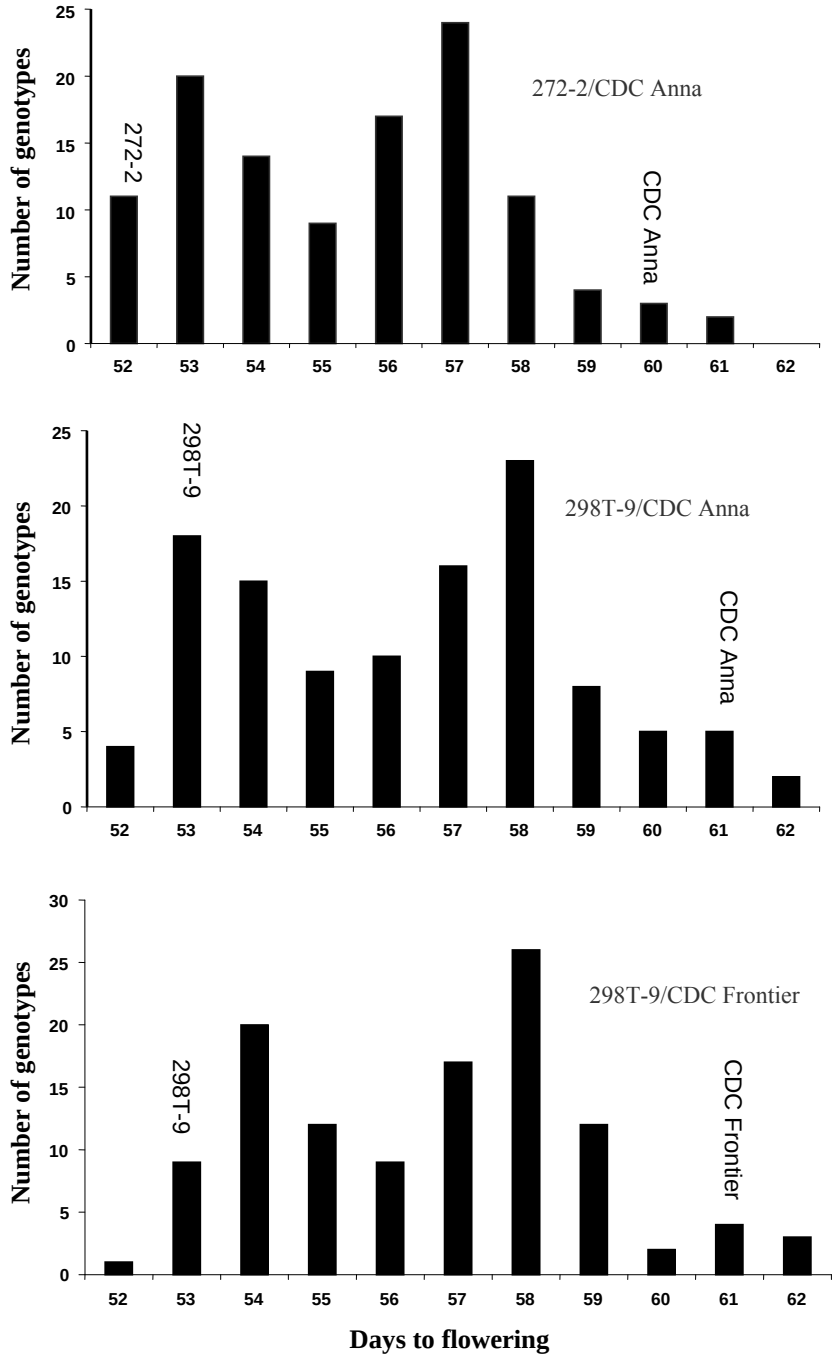

Fig. 4.3. Frequency distribution of days to flowering in three F_2 populations of chickpea evaluated at Saskatchewan Pulse Growers farm near Saskatoon in 2004.

$F_{2:3}$ families evaluated in the field were also continuous, but these followed a bimodal pattern (Fig. 4.3). Classification of the time to flowering data into early (55 days or earlier) and late (later than 55 days) did not deviate significantly from a 9 late: 7 early flowering segregation ratio (χ^2 =0.57, P = 0.45 for 272-2/CDC Anna; χ^2 = 0.89, P = 0.35 for 298T-9/CDC Anna and χ^2 = 2.26, P = 0.13 for 298T-9/CDC Frontier). This shows that time to flowering was governed primarily by two genes with duplicate recessive epistasis between them in the short-season temperate environment in western Canada.

4.3.2 Joint segregation analysis

The JSA revealed that the variation in time to flowering in chickpea was best explained by mixed two major-genes plus polygenes model class (Table 4.3), confirming the evidence from the frequency distribution pattern of the $F_{2:3}$ populations indicated above. Model E-1 had lowest AIC for the 272-2/CDC Anna and 298T-9/CDC Anna populations, whereas model E-2 did for the 298T-9/CDC Frontier population. The difference is that in model E-1 there is interaction between the two major genes, but model E-2 assumes additive-dominant type of gene action. However, the segregation pattern in F_2 vs F_3 and in $F_{2:3}$ families shown above indicated the involvement of epistatic gene action in all the three populations.

The majority of the variation in time to flowering was accounted for by the two major genes (Table 4.4). The contribution of polygenes to the total phenotypic variation was very low. Heritability of major genes was high, greater than 65% across generations and crosses. For both major genes, the late flowering alleles showed dominance over early flowering as depicted by negative values for dominance effects.

Table 4.3. Akakie's Information Criteria (AIC) values under various genetic models for time to flowering in three chickpea crosses.

	Population				Population		
Model[Z]	I	II	III	Model[z]	I	II	III
A-1	1277.0	1396.7	1340.5	D	1198.9	1304.6	1240.6
A-2	1289.7	1392.7	1391.9	D-1	1215.8	1325.7	1259.4
A-3	1371.8	1439.8	1455.6	D-2	1229.8	1339.6	1276.6
A-4	1323.3	1449.5	1394.6	D-3	1222.5	1337.7	1319.6
B-1	1196.4	1331.3	1306.6	D-4	1213.8	1332.3	1257.8
B-2	1216.4	1298.4	1248.1	E	1197.5	1283.3	1211.1
B-3	1218.1	1357.1	1340.0	E-1	<u>1193.8</u>	<u>1282.1</u>	1221.5
B-4	-	-	-	E-2	1246.4	1341.0	<u>1199.2</u>
B-5	1339.6	1406.7	1433.3	E-3	1258.8	1304.2	1304.7
B-6	-	-	-	E-4	1281.5	1406.1	1323.4
C	1234.9	1345.4	1281.6	E-5	1219.4	1334.8	1215.9
C-1	1281.9	1406.8	1323.7	E-6	1281.8	1406.8	1323.7

[z] Complete description given in Table 4.2, dash indicates that the model did not converge.

I - 272-2/CDC Anna, II - 298T-9/CDC Anna, III - 298T-9/CDC Frontier .

Lowest AIC value in each cross underlined, so is the best fitting model.

Table 4.4. Estimates of genetic parameters of time to flowering (days) in three crosses of chickpea.

1st order	Estimates			2nd order	Estimates in F_2			Estimates in $F_{2:3}$		
parameter	I	II	III	parameter	I	II	III	I	II	III
m	54.64	54.0	57.7	Σ^2_p	4.66	8.46	10.6	4.19	5.84	9.6
d_1	0.63	1.24	4.18	σ^2_{mg}	3.03	7.68	9.6	3.16	5.69	8.2
d_2	0.60	-0.24	2.15	Σ^2_{pg}	0.00	0.03	0.0	0.87	0.07	1.3
h_1	-1.75	-3.77	-6.72	Σ^2_e	1.63	0.76	1.0	0.16	0.08	0.1
h_2	-1.78	-1.33	-2.16	H^2_{mg} (%)	65.0	90.7	90.4	75.4	97.5	85.6
i	2.50	3.10	-	H^2_{pg} (%)	0.00	0.35	0.0	20.7	1.21	13.3
j_{12}	0.16	-0.25	-							
j_{21}	0.11	1.01	-							
l	0.08	-1.54	-							
[a]	2.61	2.87	-1.75							
[d]	5.60	13.2	12.5							

I - 272-2/CDC Anna, II - 298T-9/CDC Anna, III - 298T-9/CDC Frontier .

m- population mean, d_1- additive effect of major gene 1, d_2- additive effect of major gene 2, h_1- dominance effect of major gene 1, h_2- dominance effect of major gene 2, i- additive x additive epistasis, j_{12}- additive x dominance epitasis, j_{21}- dominance x additive epitasis, l- dominance x dominance epistasis, [a]– additive effect of polygenes, [d]- dominance effect of polygenes, σ^2– variance, mg– major gene, pg- polygenes, e- environment, H^2- heritability.

4.4 Discussion

Analysis of the genetic basis of time to flowering in chickpea contributes to our understanding of its inheritance mechanism and is of practical importance because the choice of effective selection/breeding methods depends in part upon the genetic basis of the trait. The JSA estimates genetic parameters for major gene(s) and polygenes and reveals gene interactions more specifically than the traditional genetic analysis for quantitative traits.

The present study revealed that time to flowering in chickpea in high latitude cool season environment of western Canada followed a two major-genes plus polygenes mixed inheritance model. The two major genes determined the majority of the phenotypic variation (> 65%) for this trait and the contribution of polygenes was minimal. Previous reports on the inheritance of time to flowering in chickpea were inconsistent, and all came from short-day, warm-temperature environments. In a preliminary report from India, based on crosses among the early (ICCV 2) and two late (GL769, BG276) parents, Gumber and Sarvjeet (1996) proposed that time to flowering was controlled by duplicate genes. However, using the same early flowering parent ICCV 2, Kumar and van Rheenen (2000) found a single major gene plus polygenes mode of inheritance for time to flowering. Or et al. (1999) also reported a single major gene for time to flowering, supporting the latter finding.

ICCV 96029, which was an indirect source of early flowering alleles for our populations, was developed from a cross of two early flowering genotypes, ICCV 2 and ICCV 93929 (Kumar and Rao, 2001). It was about one week earlier than either of the parents at ICRISAT, Patancheru, India (Kumar and Rao, 2001). This genotype likely

has additional alleles for early flowering, which strongly supports the present finding. The duration from sowing to flowering in other legumes such as common bean (*Phaseolus vulgaris*) and pigeonpea (*Cajanus cajan*) is also under the control of two genes (eg. Craufurd et al., 2001; Kornegay et al., 1993).

Time to flowering is determined by three factors: response to photoperiod (usually the most important factor), response to temperature, and 'earliness per se' genes (Snape et al., 2001). There was not sufficient information from this research to determine to which group the two major genes detected in this study belong. But, physiological studies revealed that time to flowering is a function of temperature and photoperiod in chickpea (Roberts et al., 1985) and the two major genes detected may each respond to either or both factors. Snape et al. (2001) also reported that different major genes controlled temperature and photoperiod effects on time to flowering, and that 'earliness per se' is generally considered a QTL in wheat.

Estimates of genetic parameters provide an indication of the relative importance of the different types of gene effects affecting the total genetic variation (Hayman, 1958). In this study, epistatic gene effects were present in sufficient magnitude to be considered important. The estimates of the additive x additive gene effects have greater relative magnitude than the other two types of digenic epistasis (additive x dominance and dominance x dominance) for this trait. Additive x additive epistasis is generally fixable, but requires delayed or later generation selection. Arshad et al. (2003) also noticed epistatic gene effects for time to flowering in chickpea. However, Malhotra and Singh (1989) did not observe epistasis for any of the important agronomic

traits including days to flowering. The differences in results were probably due to the differences in allelic constituents of the parental genotypes used.

The detection of major genes for time to flowering in chickpea demonstrates that this trait can easily be incorporated into the desired genetic background. The backcrossing or single seed descent breeding methods could effectively be deployed to advance time to flowering in chickpea. Our results showed that incorporation of these two alleles advanced flowering date by about one week under western Canadian conditions at latitude 52^0N. This effect would likely be greater under short day environments at lower latitudes, where flowering is greatly delayed for late (more photoperiod sensitive) genotypes. Hence, these two alleles play an important role in accelerating flowering time in chickpea.

Chickpea is a highly indeterminate species and early flowering may extend the duration of the reproductive period (Subbarao et al., 1995). In short-season temperate environments of western Canada, the duration of reproductive period is determined by the commencement of flowering and the end-of-season frost that terminates seed setting and growth. A longer reproductive period, brought about by early flowering alleles, could enhance seed yield in chickpea by allowing formation of a relatively large number of pods, and through longer grain filling duration (Or et al., 1999). Therefore, more progress could be made with respect to yield and earliness by incorporating the two early flowering alleles reported herein into adapted genetic backgrounds.

5. Heritability and Predicted Gain from Selection in Components of Crop Duration in Divergent Chickpea Cross Populations

Summary

Genetic analysis of ten quantitative traits related to crop duration in chickpea was carried out using three F_2 sib-populations: 272-2/CDC Anna, 298T-9/CDC Anna and 298T-9/CDC Frontier. Also, 112 recombinant inbred lines (RILs) of chickpea cross ICCV 2/JG 62 were evaluated for days to flowering, days to maturity and reproductive period. An analysis of the F_2 population data using the mixed model approach revealed that the additive component of variance was significant for days to flowering, days to first podding and days to first pod maturity, while dominance genetic variance was significant for morphological components of crop duration such as height to first pod and height at flowering. A moderate heritability estimate of 46% was obtained for both days to flowering and maturity. The predicted gain from selection as a percentage of the population mean was low (< 5%) for the key components of crop duration, days to flowering and days to maturity and reproductive period, owing to the low variability detected within the populations. To maximize gain from selection in these traits, it is therefore essential to increase genetic variability among the progenies, potentially through multi-parent crosses that may involve gene introgression from across desi and kabuli types of chickpea and from wild progenitors.

5.1 Introduction

Chickpea is an annual, self-pollinated, diploid (2N = 16) grain legume crop grown in a wide range of environments including the Mediterranean, South and West Asia, North America, and East Africa. Earliness of crop maturity is important in the avoidance of damage due to frost, drought, or disease in chickpea across these diverse environments. Earliness plays a central role in genotype adaptation to current and new environments and cropping systems and has a powerful effect on yield and yield stability (Kumar and Abbo, 2001). As a result, early maturity continues to be one of the major chickpea breeding objectives worldwide.

The duration of crop maturity in chickpea is the end result of several phenological and morphological variables, which are interrelated and which could be manipulated separately in the breeding process (Kumar et al., 1999). These include days to flowering, days to first podding, pod establishment period, days to first pod maturity, pod filling period, days to maturity, reproductive period, number of nodes to first pod, height to the first pod, height at flowering, increase in height after flowering and others. Under circumstances where recording of the maturity date of genotypes is difficult due to forced maturation by drought or frost, some of these parameters may be used to discriminate between early and late genotypes. Generally, breeders have used days to flowering as a key indicator of maturity duration (Kumar and Abbo, 2001); however, additional gains may be possible by exploiting variation in other components. Moreover, effective alteration of final maturity duration would best be achieved by selecting for more than one component of crop duration.

The effectiveness in manipulation of the components of crop duration in part depends upon understanding of the genetic bases of these traits. Of particular importance to plant breeders is the proportion of the observed variability which is heritable. This determines above all the breeding methods to be used and the intensity of evaluation required to bring about rapid changes in the respective traits (Dudley and Moll, 1969). Information on predicted genetic gain from selection is also useful in predicting the progress that can be made through breeding/selection.

Remarkable progress has been made in determining the genetic control of economically important traits for many crops in the latter half of the twentieth century. Studies in chickpea showed that days to flowering was predominantly under the control of additive genetic variance (Gowda and Bahl, 1978; Singh et al., 1992; Singh et al., 1993; Kumar et al., 1999) while both additive and nonadditive variance components were important for days to maturity (Singh et al., 1993). On the other hand, Dhaliwal and Gill (1973) and Bhat and Singh (1980) showed that variance type was predominantly nonadditive for the earliness traits in chickpea. Kidambi et al. (1988) also observed duplicate epistasis for both days to flowering and maturity. These studies were concentrated primarily in the semi-arid tropical environments and information was mainly generated indirectly from estimates of specific and general combining ability. According to Muehlbauer and Singh (1987), estimates of genetic parameters from specific and general combining ability analysis are influenced by the population used and inference to other chickpea parental lines and segregating populations may be invalid. Therefore more information on the genetics of components of crop duration from different genetic populations and environments is required to predict the

usefulness of these traits in breeding programs. The objective of this study was to estimate heritability and genetic gain from selection for key components of crop duration in chickpea in the short-season temperate environment of western Canada.

5.2 Materials and Methods

5.2.1 Early generation segregating populations

Three crosses were made during winter 2002 at the University of Saskatchewan, Saskatoon, Canada. These were 272-2/CDC Anna, 298T-9/CDC Anna and 298T-9/ CDC Frontier. Genotypes 272-2 and 298T-9 have small seed size with early flowering characteristics. CDC Anna and CDC Frontier are commercial genotypes developed for Saskatchewan with medium time to flowering under western Canadian conditions (Vandenberg et al., 2003; Warkentin et al., 2005b). All the parental genotypes belong to the desi type of chickpea except CDC Frontier, which belongs to the kabuli type. The F_1 generation was grown under greenhouse conditions and advanced to F_2, which was subsequently used for genetic study.

Greenhouse experiment

Seeds of F_2 generation from four random F_1 plants of each cross were grown individually in 20 cm diameter pots in a greenhouse in the summer 2003. The term 'cohort' is used hereafter to indicate plants coming from one mother F_1 plant. Thus, four cohort groups were used from each cross in this study. The two parental genotypes were also included. The experiment was set up in three replications. Fifteen contiguous

cohorts were present in each replication, whereas the parents were represented by four plants per replication. Altogether, the experiment consisted of 180 individual F_2 plants (4 cohort groups x 15 plants/cohort x 3 replications) and 24 parental pots (2 parents x 4 duplicates/replication x 3 replications) from each cross.

For the evaluation of the F_2 generation the pots were filled with Redi-Earth soil (W.R. Grace and Co., ON, Canada). Photoperiod was maintained at 16 hours and mean air temperature was $24 \pm 3\ ^0$C. Fast release (20N: $20P_2O_5$: 20 K_2O) (CHISSO-ASAHI fertilizer Co. Ltd, Tokyo, Japan) fertilizer was applied at a rate of 5 g pot^{-1} one week after emergence and at 35 g pot^{-1} of controlled release type 100 (14N: $14P_2O_5$: $14K_2O$) (Plant Products Co. Ltd, ON, Canada) another week later. Watering was conducted every 3─7 days depending on crop growth stage and corresponding water use. Data for days to flowering (number of days from seeding to appearance of first flower), days to first podding (number of days from seeding to appearance of first fully developed pod), days to first pod maturity (number of days from seeding to when the lowest pod turned brownish), percent pod maturity (percentage of matured pods at four months after seeding), pod establishment period (days to first podding ─ days to flowering), pod filling period (days to first pod maturity ─ days to first podding) were recorded. Morphological components of crop duration: number of nodes to first pod (number of nodes to the most bottom pod on the main stem), height to first pod (height of the first podding node on the main stem), height at flowering (plant height at flowering stage), and increase in height after flowering (increase in height between flowering and maturity stages), were determined.

Field experiment

In 2004, 115 $F_{2;3}$ families were evaluated at the Saskatchewan Pulse Growers farm near Saskatoon (52.1^0N, 106.4^0W). These were derived from individual F_2 plants grown in a greenhouse. The experiment was laid out in an ARCBD using the parents as replicated checks (Federer, 1956). Plot size was two rows of 1 m length. Seeds were treated with a mixture of Apron FL (317 g L^{-1} metalaxyl) at a rate of 32 mL kg^{-1} seed and Crown (92 g L^{-1} carbathiin and 58 g L^{-1} thiabendazole) at a rate of 6 mL kg^{-1} seed to protect against seedling diseases. *Mesorhizobium ciceri* granular inoculant (Becker Underwood Inc., IW, USA) was applied in the seed rows at a rate of 5.6 kg ha^{-1}. Weeds were controlled using fall application of Pursuit (240 g L^{-1} imazethapyr) at a rate of 69 mL ha^{-1} plus Edge (5% ethalfluralin) at a rate of 28 kg ha^{-1}. The crop was protected against the fungal disease ascochyta blight using the fungicides Bravo 500 (500 g L^{-1} chlorothalonil) at a rate of 3.2 L ha^{-1} and Headline (250 g L^{-1} pyraclostrobin) at a rate of 395 mL ha^{-1}. Bravo 500 was applied at the time chickpea plants began flowering, followed 10 days later by Headline, then another 10 days later by a second application of Headline. Data were collected on traits found important in the initial study including days to flowering, days to first pod maturity, percent pod maturity at four months after seeding, height at flowering, and increase in height in height after flowering as shown above for the greenhouse experiment. The 2004 season was cooler and wetter than average and crop maturity was delayed. Populations 298T-9/CDC Anna and 298T-9/CDC Frontier were too late maturing to take meaningful data on maturity traits, thus genetic analysis was conducted only for the relatively early 272-2/CDC Anna population.

The F_2 populations evaluated in a greenhouse were subjected to analysis of genetic effects using the mixed linear model approaches (Wu et al., 2003). An additive-dominance model was fitted and the significances of genetic parameters were tested using jackknifing techniques (Miller, 1974). Data from the field experiment were analyzed using SAS PROC GLM (SAS Institute Inc., 1999) following the description given by Scott and Milliken (1993). Genetic variability for days to flowering, days to first pod maturity, height at flowering and increase in height after flowering was assessed. Also, Pearson correlation coefficients among these earliness traits were determined.

5.2.2 Recombinant inbred lines

One hundred and twenty one chickpea genotypes including 112 RILs, their two parents and seven chickpea varieties developed for western Canada were grown at Brooks (50.3^0N, 111^0W), Alberta in summer 2003. Plot size was three rows of 1m length. The RILs were developed from a cross between JG 62 and ICCV 2 at ICRISAT (Kumar and van Rheenen, 2000). These were laid out in an 11 x 11 partially balanced square lattice design. The crop was protected against ascochyta blight with applications of Brovo 500 (500 g L^{-1} chlorothalonil) at a rate of 3.2 L $ha^{-1}$and latter Quadris (250 g L^{-1} azoxystrobin) at a rate of 0.49 L ha^{-1}. The 2003 season was generally warm and dry permitting full crop maturity before first frost in the region. Data were also collected on days to flowering, days to maturity and reproductive period (days to maturity ─ days to flowering). Data on agronomic traits such as plant height (cm) and 100 seed weight (g) were also collected and included for comparison purpose.

Analysis of variance was carried out using SAS statistical packages using PROC LATTICE (SAS Institute Inc., 1999) with the presumed experimental model:

$$Y_{ijk} = \mu + g_i + \alpha_k + \beta_{jk} + \in_{ijk}$$

Where μ is the overall mean, g_i is effect of the i^{th} line, α_k is the effect of k^{th} replication, β_{jk} is effect of the j^{th} block within the k^{th} replication, and $\in_{ijk}$ is the residual.

Genotypic variance (σ^2_g) and phenotypic variance ($\sigma^2_p = \sigma^2_g + \sigma^2_e$) were resolved based on expected mean squares shown in Table 5.1. Genetic coefficient of variation (GCV %) was calculated as percentage of the square root of genetic variance to population mean for each trait. The ratio of genetic variance to the total phenotypic variance was taken as heritability. Predicted genetic advance (GA) was calculated as given by Falconer (1989):

$$GA = k \times h^2 \times \sigma_p$$

where k is a selection differential for which 2.06 (a standardized value for 5% selection intensity) is used in this analysis and σ_p is standard deviation of the phenotypic variance.

Table 5.1. Expected mean squares for partially balanced square lattice design used in experiment II.

Source	*Df*	*Mean square*	*Expected mean square*
Replication (r)	r-1	M_r	-
Blocks $_{adj.}$ (b)	r(b-1)	M_b	-
RILs (g)	bn – 1	M_g	$\sigma^2_e + r\sigma^2_g$
Error (e)	nr (b-1) – (bn-1)	M_e	σ^2_e

df - degrees of freedom, n- number of entries in a block.

5.3 Results

5.3.1 Early generation segregating populations

Due to the warm temperature and long photoperiodic conditions in the greenhouse, the F_2 populations started flowering early with an overall mean days to flowering of 24 days (Table 5.2). Similarly, days to first pod maturity was relatively short with a mean of 62 days. However, substantial ranges of observations occurred among the genotypes in all the traits considered, for example days to first pod maturity ranged from 47─81 days and percent pod maturity at four months after planting ranged from 44─100% (Table 5.2). When assessed separately for each cross, the ranges for these traits were relatively larger for the kabuli x desi cross (298T-9/CDC Frontier) compared to the desi x desi (272-2/CDC Anna or 298T-9/CDC Anna) crosses.

The mixed model analysis revealed significant phenotypic and genotypic variances among the F_2 populations for most of the components of crop duration (Table 5.3). The additive genetic variance was significant for days to flowering, days to first podding and days to first pod maturity and this accounted for the large proportion of the phenotypic variance for these traits. Dominance genetic variance was significant for height at flowering and height to first pod, which are the morphological components of crop duration. Neither the additive nor the dominance component of genetic variance was significant for percent pod maturity recorded on individual F_2 plants, despite the wide phenotypic range.

Phenotypic variability among the field grown $F_{2:3}$ families was substantial for the components of crop duration (Table 5.4), as observed for the F_2 populations evaluated in the greenhouse. However, the mean number of days to reach different

phenological stages was much greater under field conditions, primarily due to the cool and wet growing conditions in 2004. Mean days to flowering and days to first pod maturity were 55 and 94 days, respectively (Table 5.4).

Phenotypic correlation coefficients in the $F_{2:3}$ generation of 272-2/CDC Anna cross are shown in Table 5.5. Percent pod maturity exhibited inverse relationship with days to flowering and days to first pod maturity, i.e., early start of flowering and maturity of lower pods were important to obtain a high percent pod maturity at four months after seeding. Height at flowering was not associated with the key components of crop duration considered. However, increase in height after flowering was positively and negatively associated with days to first pod maturity and percent pod maturity, respectively, implying that less growth in height after flowering was important for earlier crop maturity.

Table 5.2. Variability for some earliness parameters in three chickpea F_2 populations evaluated under greenhouse conditions.

Parameter		*272-2/CDC Anna*	*298T-9/CDC Anna*	*298T-9/CDC Frontier*
Days to flowering	Mean	24	24	24
	Range	18─28	19─28	19─29
	GCV	6.8	8.1	9.4
Days to first pod maturity	Mean	60	62	63
	Range	52─70	50─81	47─80
	GCV	6.3	7.6	10.6
Percent pod maturity	Mean	85	86	84
	Range	56─100	50─100	44─100
	GCV	13.4	14.5	15.5

GCV – genetic coefficient of variability

Table 5.3. Estimates of variance components for components of crop duration using a mixed model approach in F_2 sib-populations of chickpea crosses 272-2/CDC Anna, 298T-9/CDC Anna and 298T-9/CDC Frontier evaluated in the greenhouse in summer 2003.

	Populatio	*Components of variance*			
Trait	*n mean*	Additive	Dominance	Residual	Phenotypic
Days to flowering	24	1.86*	0.00	3.63**	5.48**
Days to first podding	29	2.48*	0.21	4.67**	7.36**
Pod establish. period (days)	5	0.0	0.31	0.86*	1.17**
Days to first pod maturity	63	14.26*	11.27	24.13**	49.66**
Pod filling period (days)	38	3.60	13.71	17.01**	34.32*
Percent pod maturity (%)	87	2.21	14.82	148.37*	165.40**
No. of nodes to first pod	14.1	0.45	1.26	3.58**	5.29**
Height to first pod (cm)	22.1	2.31	19.51*	18.76**	40.58*
Height at flowering (cm)	26.3	0.0	26.30*	22.67**	48.97**
Increase in height after flowering (cm)	16.7	0.0	13.67	35.04**	48.71*

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

Table 5.4. Mean, range and phenotypic variance for components of crop duration in $F_{2:3}$ families of chickpea cross 272-2/CDC Anna (N= 115) evaluated at Saskatchewan Pulse Growers farm near Saskatoon in 2004.

Trait	*Mean*	*Range*	[z] *Phenotypic variance* (σ^2_g)
Days to flowering	55	52 - 61	4.26**
Days to first pod maturity	94	77 - 110	42.58**
Percent pod maturity (%)[y]	66	25 - 85	224.64**
Height at flowering (cm)	39	29 - 48	15.33**
Increase in height after flowering (cm)	23	10 - 33	27.58**

[z] Obtained from genotype mean square in the analysis of variance.

[y] Assessed at four month after seeding

** Significant at P < 0.01.

Table 5.5. Pearson correlation coefficients among traits related to earliness in $F_{2:3}$ families of chickpea cross 272-2/CDC Anna (N= 115) evaluated at Saskatchewan Pulse Growers farm near Saskatoon in 2004.

Trait	*DFPM*	*PPM*	*HF*	*IH*
DF	0.42**	- 0.35**	0.05	0.18
DFPM	-	- 0.71**	0.01	0.51**
PPM		-	- 0.05	- 0.49**
HF			-	- 0.11

DF - days to flowering, DFPM - days to first pod maturity, PPM - percent pod maturity, HF - plant height at flowering, IH - increase in plant height after flowering.

** Significant at P < 0.01.

5.3.2 Recombinant inbred lines

Significant differences were observed among the RILs in days to flowering, days to maturity and reproductive period (Table 5.6). The source of this variation was partly genetic, but the magnitude of the genetic component of variance was relatively small for days to flowering, days to maturity and reproductive period (Table 5.7). As a result, genetic coefficient of variation (GCV) was less than 5% for these traits.

The heritability value for days to flowering was 46%, which was in agreement with the significant additive genetic variance obtained for this trait in F_2 populations (Tables 5.3 and 5.8). Days to maturity was also moderately heritable (46%). Predicted genetic advance as a percentage of the population mean was low (< 5%) for days to flowering, days to maturity and reproductive period due to the low magnitude of variability displayed among the RILs (Table 5.7). Both heritability and genetic advance were substantially high for plant height and 100 seed weight (Table 5.8).

Table 5.6. Mean squares of some components of crop duration and related agronomic traits in recombinant inbred lines (RILs) of chickpea cross ICCV 2/JG 62 evaluated at Brooks, AB in 2003.

Sources of		*Mean squares*				
variation	*df*	DF	DM	RP	PTHT	100 SW
Replication	1	0.037	0.335	0.595	83.322	0.007
Blocks	20	2.601	13.430	14.050	8.431	2.552
RILs	120	6.164**	15.316**	12.877**	37.264**	50.455**
Error	100	2.274	5.696	6.684	7.960	1.731

DF - days to flowering, DM - days to maturity, RP - reproductive period, PTHT - plant height, 100 SW - hundred seed weight. ** Significant at $P < 0.01$.

Table 5.7. Phenotypic, genotypic and environmental variances and genetic coefficients of variation (GCV) for some components of crop duration and related agronomic traits in recombinant inbred lines (RILs) of chickpea cross ICCV 2/JG 62 evaluated at Brooks, AB in 2003.

					PTHT	*100 SW*
	Variable	*DF*	*DM*	*RP*	*(cm)*	*(g)*
	RILs	41	83	42	28	26
Mean	ICCV 2	40	82	42	28	32
	JG 62	41	85	44	26	21
Phenotypic variance (σ^2_p)		4.2	10.5	9.8	22.6	26.1
Genotypic variance (σ^2_g)		1.9	4.8	3.1	14.6	24.4
Error variance (σ^2_ϵ)		2.3	5.7	6.7	8.0	1.7
GCV (%)		3.4	2.6	4.2	13.7	19.0

DF - days to flowering, DM - days to maturity, RP - reproductive period, PTHT - plant height, 100 SW - 100 seed weight.

Table 5.8. Estimates of heritability (h^2) and predicted genetic advance (GA) as a percent of the population mean for components of crop duration and related agronomic traits in recombinant inbred lines of chickpea cross ICCV 2/JG 62 evaluated at Brooks, AB in 2003.

Trait	*h^2 (%)*	*GA (%)*
Days to flowering	46	4.7
Days to maturity	46	3.6
Reproductive period (days)	32	4.9
Plant height (cm)	65	22.7
100 seed weight (g)	93	37.8

5.4 Discussion

Knowledge of the relative contributions of genetic components and environmental effects in controlling the variation for different quantitative traits is helpful for crop improvement (Kumar et al., 1999). This information allows geneticists and breeders to employ improved strategies to develop more efficient selection methods and genetic populations (Nyquist, 1991). The present study generated heritability estimates from variance component analysis for divergent chickpea cross populations, different from previous research on this crop which generally concentrated on diallel crosses (Malhotra and Singh, 1989; Singh et al., 1992; Kumar et al., 1999). According to Tefera et al. (2003), accumulation of heritability information for traits from different genetic populations is useful to ascertain its true magnitude.

Since chickpea is a highly inbreeding species, additive genetic variation is needed by breeders aiming to improve quantitative traits (Muehlbauer and Singh, 1987). It was evident from the present study that additive genetic variance was significant for days to flowering, days to first podding and days to first pod maturity. This complements other studies which have reported a preponderance of additive variance for days to flowering (Malhotra and Singh, 1989; Singh et al., 1992; Singh et al., 1993; Kumar et al., 1999) and days to first podding (Kumar et al., 1999). Heritability estimate was 46% for both days to flowering and days to maturity, which is reasonably high as compared to the lower values frequently reported for traits related to fitness (eg. Falconer, 1989).

Chickpea maturation often occurs under unfavorable environmental conditions that are either too cool and wet in temperate environments or too dry in semi-arid

tropics. As a result evaluation for days to maturity is untenable and generally breeders have used days to flowering as an indicator of crop duration. In practice, early flowering genotypes do not necessarily mature early, and some late flowering genotypes have a short reproductive period and mature simultaneously with earlier flowering ones (Summerfield and Roberts, 1988). Days to first pod maturity and percent pod maturity rated before the occurrence of frost damage appears to be useful in discriminating between early and late genotypes. However, since early flowering leads to early onset of reproductive growth, combined selection for days to flowering, days to first pod maturity and percent pod maturity would enable more gain in improving earliness of crop maturity. Since significant association was observed between these traits, simultaneous improvement of days to flowering, days to first pod maturity and percent pod maturity should be feasible.

A pronounced environmental effect and corresponding high residual variance was found in percent pod maturity for the F_2 populations evaluated on individual plants (Table 5.3). Chickpea is extremely sensitive to excess water availability and this may have interfered with the maturation process in some pots in this experiment, obscuring the precise determination of the genetic component of variance. Under environmental stress, the phenotypic variance of sensitive traits would generally increase more rapidly than the genotypic variance and the latter value would be overshadowed (Collaku and Harrison, 2005). Early generation selection may be effective for percent pod maturity, but due to environmental sensitivity of this trait it may not be amenable to selection among individual F_2 plants. Selection for percent pod maturity may be more effective when based on F_2-derived families than individual plants.

Heritability estimates were moderately high for the key components of crop duration: days to flowering, days to maturity and reproductive period, but the predicted genetic advance as a percentage of the population mean was generally low (Table 5.8). The low genetic advance was mainly attributed to low variability within the populations. Parental genotypes and the recombinants created were not widely different for the components of crop duration. Genetic coefficient of variation was no more than 5% for days to flowering, days to maturity and reproductive period in agreement with the finding of Kidambi et al. (1988). Conventional and molecular genetic studies have indicated low genetic variability in chickpea (eg. Ahmad and Slinkard, 1992). This implies that emphasis should be given to the creation of genetic variability to maximize gain from selection in components of crop duration in chickpea. Genetic variability is a basic requirement for genetic improvement of a crop.

As a part of the strategy to increase genetic variability in chickpea, and thereby make the desired changes in earliness of crop maturity, wide and complex crosses might be sought. Although comparatively more time is spent during hybridization to generate multiple-parent crosses, the process allows production of recombinants with favorable alleles coming together (Singh, 2001). Several lines of evidence showed that greater genetic distance between parental lines results in higher genetic variance among the progeny in economically important traits in chickpea (Maynez et al., 1993), wheat (Busch et al., 1974), dry bean (Ghaderi et al., 1984) and peanut (Arunachalam et al., 1984). Chickpea crosses may need to involve gene introgression from across desi and kabuli types and from wild relatives, with subsequent backcrossing to the commercial (recurrent) parent. In this way, breeders could better tailor earliness of crop maturity,

which is a very desirable agronomic trait in chickpea in the short-season temperate environment of western Canada.

In summary, this study employed a more appropriate mixed model approach for the genetic analysis of earliness traits in chickpea, than previously published reports and added upon existing knowledge of the genetic control of these traits. Information generated on the genetic control of several phenological and morphological components of crop duration: days to first podding, pod establishment period, days to first pod maturity, pod filling period, percent pod maturity, reproductive period, number of nodes to first pod, height to first pod, height at flowering, increase in height after flowering, could be used to manipulate them separately in the breeding process and then ultimately to reduce the duration of crop maturity.

6. Post-flowering Dry Matter Accumulation and Partitioning and Timing of Crop Maturity in Chickpea in Western Canada

Summary

A field experiment aimed at determining whether timing of crop maturity was related to patterns of dry matter accumulation and partitioning to reproductive organs in chickpea was conducted at different locations in Saskatchewan over two seasons, 2003 and 2004. Five genotypes 272-2, 298T-9, E100Ym, CDC Anna, and CDC Frontier were grown in a RCBD with four replications. Beginning at 60 days after seeding and every 15 days following, plant samples were taken and separated into stem, leaf and pod fractions. Then dry weights of the sample fractions were determined. Total dry matter production showed an increasing trend over sampling dates, but the increase was at a decreasing rate beginning in mid-season. The early genotype 272-2 had a similar pattern of total dry matter accumulation as others, but had significantly smaller vegetative (stem plus leaf) dry matter accumulation during the latter part of the growth period. These results show that there was a continued assimilation and increase in total dry matter, but the mid to late season assimilate was mostly partitioned to pods for genotype 272-2. Also, there were systematic differences among genotypes in dry matter partitioning to pods and pod harvest index in parallel with their differences in maturity duration. This research shows that assimilate partitioning in ways that provide optimal proportion of pod dry matter is important for achieving early maturity in chickpea in western Canada.

6.1 Introduction

Chickpea is a grain legume crop which is best adapted to the semi-arid tropics and the Mediterranean region (Jettner et al., 1999). This crop was recently introduced to western Canada and faces a unique challenge. It is one of few production regions in the world where chickpea matures under conditions of declining temperature. This coupled with end-of-season precipitation in some years exacerbates the indeterminate nature of the crop and delays maturity. In this environment, the chickpea crop is often exposed to frost damage resulting in reduced yield and quality.

A determinate growth habit, in which vegetative growth ceases at flowering, could be useful in environments where growing conditions often lead to excessive plant canopy development (van Rheenen et al., 1994). In this case, post-flowering vegetative growth would be restricted, thus enabling synchronized maturity of pods. Unfortunately the determinate growth habit is lacking in chickpea germplasm. Van Rheenen et al. (1994) induced determinacy in chickpea through mutation; however, this line was indeterminate when grown in Saskatchewan.

In accordance with the nutritional hypothesis, crop maturity duration in indeterminate species is a function of the time when the pod load that is already growing monopolizes current assimilates and precludes the production of new podding sites (Bange and Milroy, 2004). Hearn (1972) also pointed out that when the reproductive sink uses the available assimilate supply, production of stem and leaves would cease, thus leading to early crop maturation. This implies that assimilate partitioning in ways that provide an optimal proportion to reproductive parts is essential

for achieving early maturity. Apparently, Bange and Milroy (2000) observed that an early cotton genotype partitioned a greater proportion of dry matter to the fruit early in the fruiting cycle compared to a late maturing genotype. Pace et al. (1999) also showed that the key trait driving maturity was the preferential partitioning of dry matter to the fruit in cotton. This was supported by the observation of inverse relationship between harvest index and time to maturity in many crop species (Schapaugh and Wilcox, 1980; Wallace et al., 1993).

Growth analysis in chickpea revealed genotypic differences in the pattern of dry matter accumulation and partitioning to reproductive parts, within the prevailing weather conditions and management practices (Khanna-Chopra and Sinha, 1987; O'Toole et al., 2001). Williams and Saxena (1991) observed marked differences among 120 chickpea genotypes assessed for crop growth rate and efficiency of dry matter partitioning to the seed. Further, Shamsuzzaman et al. (2002) showed that an early maturing mutant chickpea genotype 'Hypersola' had significantly lower amounts of dry matter in the leaf and stem fractions during its last few weeks of growth as compared to its later maturing parental genotype. These variable strategies of growth available within the chickpea germplasm may partly underlie differences in adaptation and yield in this crop.

The underlying theme of chickpea breeding in western Canada is to maximize grain yield within the short growing season, while allowing the crop to reach harvest maturity before the occurrence of early fall frost. A clear understanding of strategies that different chickpea genotypes adopt in their growth behavior under western Canadian conditions is important for fine-tuning the maturity duration and to optimize

yield within the short growing period. Particularly information on both the pattern of post-flowering (i.e. the period during which yield formation occurs) dry matter accumulation and the priorities with which this dry matter is partitioned into structures such as leaves, stems, and pods are useful. This information is important to determine the specific changes required in growth strategies to allow timely maturity in chickpea in this environment. The objectives of the present study were 1) to determine the pattern of post-flowering dry matter accumulation and partitioning to vegetative and reproductive parts in diverse chickpea genotypes in the short-season temperate environment of western Canada, and 2) to assess the relationship of the patterns of dry matter accumulation and partitioning with the timing of crop maturity.

6.2 Materials and Methods

6.2.1 Genotypes and experimental set-up

Field experiments were conducted at four site-years in Saskatchewan, Canada (i.e., Goodale in 2003, Goodale, Preston and Swift Current in 2004). Goodale and Preston are near Saskatoon (52.1^{o}N, 106.4^{o}W), and Swift Current is at 50.6^{o}N, 107.4^{o}W. Soil type was Dark Brown at Goodale and Preston, and Brown type at Swift Current.

Five genotypes varying in some important morphophenological traits were used for this investigation. These were 272-2, 298T-9, E100Ym, CDC Anna and CDC Frontier. The first two are breeding lines from the Crop Development Centre, University of Saskatchewan, with key characteristics of early flowering and relatively

small seed size (< 20 g 100 seeds^{-1}). CDC Anna (Vandenberg et al., 2003) and CDC Frontier (Warkentin et al., 2005b) are genotypes developed for production in Saskatchewan. They have large seed size and are relatively late to flower. E100Ym, which was obtained from ICRISAT, is a short internode germplasm with large seed size (Sandhu et al., 1990). Genotypes 272-2, 298T-9, E100Ym, and CDC Anna belong to the desi chickpea type, whereas CDC Frontier is a kabuli type.

The five genotypes were arranged in a RCBD with four replications. Seeding was conducted on 16 May, 17 May, 19 May, and 25 May at Goodale 2003, Swift Current 2004, Preston 2004 and Goodale 2004, respectively. Each genotype was seeded in four row plots with 4 m row length. Spacing was 30 cm between rows and a target population density of 44 plants m^{-2} was used as recommended for western Canada (Gan et al., 2003). Seeds were treated with a mixture of Apron FL (317 g L^{-1} metalaxyl) at a rate of 32 mL kg^{-1} seed and Crown (92 g L^{-1} carbathiin and 58 g L^{-1} thiabendazole) at a rate of 6 mL kg^{-1} seed to protect against seedling diseases. *Mesorhizobium ciceri* granular inoculant (Becker Underwood Inc., IW, USA) was applied in the seed rows at a rate of 5.6 kg ha^{-1}. Weeds were controlled using fall application of Pursuit (240 g L^{-1} imazethapyr) at a rate of 69 mL ha^{-1} plus Edge (5% ethalfluralin) at a rate of 28 kg ha^{-1}. The crop was protected against the fungal disease ascochyta blight using the fungicides Bravo 500 (500 g L^{-1} chlorothalonil) at a rate of 3.2 L ha^{-1} and Headline (250 g L^{-1} pyraclostrobin) at a rate of 395 mL ha^{-1}. Bravo 500 was applied at the time chickpea plants began flowering, followed 10 days later by Headline, then another 10 days later by a second application of Headline.

6.2.2 Data collection and analysis

Beginning at 60 days after seeding and every fifteen days following, plant samples consisting of 0.3 m^2 areas were taken from the two central rows of each plot. The first sampling date coincided with flowering stage in 2004 and early podding stage in 2003. The plants sampled were separated into leaf, stem, and pod fractions. Pods consisted of pod walls and seeds. The samples were dried at 81^oC for 72 hours and then dry weights were determined. Data on days to 50% flowering (number of days from seeding to when 50% of the plants in a plot had at least one open flower) and days to maturity (number of days from seeding to when 90% of the pods in a plot had turned brown), seed yield (kg ha^{-1}), and 100 seed weight (g) were recorded. However, the plants were affected by frost before maturity at Goodale 2004 and Preston 2004, thus days to maturity, seed yield and 100 seed weight data are not available for these site-years. Seasonal rainfall and temperature for Saskatoon and Swift Current stations were obtained from Environment Canada (http://www.climate.weatheroffice.ec.gc.ca/ climateData/canada_e.html) and summarized in Table 6.1.

Analysis of variance was carried out on days to flowering and maturity, grain yield and 100 seed weight using SAS statistical packages (SAS Institute Inc., 1999). The Fisher's protected least significant difference (LSD) was used for the comparison of treatment means at P = 0.05. A mixed model methodology as implemented by the Mixed procedure was used to analyze the repeated measurements for amount of total (leaf + stem + pod), vegetative (leaf + stem) and pod dry matter accumulation with a REPEATED statement for sampling dates (Bowley, 1999; Littell et al., 1998). The covariance among sampling dates for the same genotype was modeled using the

autoregressive plus random effect covariance structure. Least square means of genotype effects in total, vegetative and pod dry matter were compared at different sampling dates.

Data on pod harvest index (i.e. the ratio of pod dry weight to the total aboveground dry matter) at the last sampling date was presented. Further, dry matter partitioning coefficient to the pods (Coleman et al., 1994) for the different genotypes was determined. This was estimated by the gradient of the regression of pod dry weight on total dry matter over sampling dates as previously used by Ellis et al. (2000). Pearson correlation coefficients among pod harvest index, dry matter partitioning coefficient to pods and days to maturity were determined.

6.3 Results

6.3.1 Environmental conditions and crop phenology

Seasonal precipitation and mean air temperature were variable over the two years (Table 6.1). In 2003, conditions were generally warm and dry, whereas 2004 was wet and cool, typical of a season when early maturity is essential. Over the five growing months (May─September), the total precipitation in 2004 was 16% and 20% more than the long-term averages at Saskatoon and Swift Current, respectively. Conversely, the monthly mean air temperature was consistently less in 2004 than the long term averages at both Saskatoon and Swift Current.

The variation in climatic conditions was heavily reflected in crop phenology. The genotypes flowered in 37─46 days and matured in 93─107 days in 2003 (Table 6.2). Crop growth was slow in 2004, delaying flowering by one to two weeks and maturity by more than five weeks compared to 2003. The time taken to flowering was less at Goodale than other sites in 2004 due to the slightly later planting at this site (Table 6.2). However, the crop was affected by frost before physiological maturity at this site and days to maturity data were not obtained. The same was true for the late maturing genotypes at Preston 2004.

The difference among genotypes in days to flowering and maturity was significant ($P < 0.05$) at all site-years (Table 6.2). Genotype 272-2 was relatively early to flower and mature, whereas E100Ym was the latest to mature across site-years, despite its intermediate flowering time. CDC Frontier was the latest genotype to flower, but matured at approximately the same time as 298T-9, though the latter preceded CDC Frontier by about one week in days to flowering.

Table 6.1. Monthly total precipitation and monthly mean air temperature at Saskatoon and Swift Current during May─September in 2003 and 2004.

	Months					*Total*
Season	May	June	July	August	Sept	
Precipitation (mm)						
Saskatoon 2003	16.0	19.0	48.5	30.0	25.5	139.0
Saskatoon 2004	26.5	79.7	75.0	73.5	21.0	275.7
Swift Current 2004	71.7	66.2	61.1	72.3	27.1	298.4
Long term Saskatoon	49.2	61.1	60.1	38.8	29.0	238.2
Long term Swift Current	52.0	67.9	55.2	43.5	30.6	249.2
Mean temperature (^oC)						
Saskatoon 2003	12.1	16.0	18.9	20.9	11.5	-
Saskatoon 2004	8.5	13.1	17.3	14.6	10.7	-
Swift Current 2004	8.6	12.9	17.6	15.3	12.0	-
Long term Saskatoon	11.5	16.0	18.2	17.3	11.2	-
Long term Swift Current	11.0	15.5	17.9	17.4	11.4	-

Table 6.2. Days from seeding to flowering and to physiological maturity in five chickpea genotypes across different site-years.

	Flowering				Physiological maturity		
	Goodale	Goodale	SC	Preston	Goodale	SC	Preston
Genotype	2003	2004	2004	2004	2003	2004	2004
272-2	37	47	54	50	93	129	128
298T-9	38	46	55	52	97	135	139
E100Ym	42	49	56	53	107	146	Late[z]
CDC Anna	44	53	58	56	100	139	Late[z]
CDC Frontier	46	54	59	59	97	135	142
Mean	42	50	56	54	99	135	-
LSD $_{(0.05)}$	0.9	1.1	1.0	0.8	2.6	5.0	-
CV (%)	1.3	1.4	0.9	1.0	1.7	2.0	-

[z] Affected by frost before physiological maturity.

SC – Swift Current.

Note that all genotypes were affected by frost before physiological maturity at Goodale 2004, thus maturity data were not reported.

6.3.2 Seed yield and 100 seed weight

The recently released cultivars CDC Frontier and CDC Anna were superior in seed yield at Goodale 2003 and Swift Current 2004, where yield data were obtained (Table 6.3). However, a large proportion of the seeds harvested were immature and green at Swift Current 2004, especially for the later maturing genotypes. When assessed on fully matured seeds, excluding green shriveled seeds, the early maturing genotype 272-2 was the highest yielder along with CDC Frontier at Swift Current 2004 (Table 6.3).

Differences were significant among genotypes in 100 seed weight (Table 6.3). The early genotype 272-2 was smallest in seed size, but the association between 100 seed weight and days to maturity was not significant ($r = 0.66$; $p = 0.22$ at Goodale 2003 and $r = 0.70$; $p = 0.19$ at Swift Current 2004). Seed weight was relatively higher at Swift Current 2004 than Goodale 2003 for all genotypes due to better soil moisture availability for grain filling in 2004.

6.3.3 Patterns of dry matter accumulation and partitioning

Analysis of variance revealed significant differences among genotypes and sampling dates in total, vegetative and pod dry weights at all site-years. Total dry matter showed an increasing trend over sampling dates for all genotypes, but the increase was at a decreasing rate beginning in mid-season (Fig. 6.1). All genotypes had a substantial increase in post-flowering total dry matter, with up to five-fold more total dry matter being produced by the last sampling date (i.e. 120 days after seeding) compared to the amount at the first sampling date (i.e. 60 days after seeding).

Table 6.3. Seed yield and 100 seed weight of five chickpea genotypes evaluated at Goodale in 2003 and Swift Current (SC) in 2004.

	Seed yield (kg ha^{-1})		100 seed weight (g)	
Genotype	Goodale 2003	SC 2004	Goodale 2003	SC 2004
272-2	2271	2199 (2051)	11.2	13.7
298T-9	2004	2217 (1547)	16.6	20.3
E100Ym	1492	1610 (650)	29.9	37.0
CDC Anna	2333	3278 (1216)	19.0	24.0
CDC Frontier	3479	4913 (2094)	30.6	37.3
Mean	2316	2843 (1512)	21.4	26.5
$LSD_{(0.05)}$	429	856 (507)	1.5	1.6
CV (%)	11.8	15.7 (12.3)	4.4	3.1

Figures in parentheses at SC 2004 were yield of normal, fully matured seeds. These seeds were used for 100 seed weight assessment.

Genotypes were affected by frost before physiological maturity at Goodale 2004 and Preston 2004, thus data were not reported.

Differences were evident among genotypes in total dry matter production at each sampling date at all site-years. CDC Frontier reached relatively greater maximum dry matter content than the other test genotypes. However, the amount of total dry matter accumulation was not related to the differences in maturity duration among genotypes in this experiment. Total dry matter for 272-2, 298T-9 and E100Ym were comparable across sampling dates at most site-years, despite their marked differences in maturity duration.

The pattern of vegetative dry matter accumulation over sampling dates in the five genotypes considered is shown in Fig. 6.2. Vegetative dry matter tended to increase for some time during the sampling period and then started to decline, except at the extra wet site-year Goodale 2004. The decline in vegetative dry matter started consistently later for E100Ym. The earlier maturing genotype 272-2 dropped many of its leaves as it approached maturity and generally had significantly lower vegetative dry matter at the last sampling date compared to the other genotypes.

The increase in pod dry weight across sampling dates followed a more or less linear trend for all genotypes (Fig. 6.3). As expected, the rates of increase in pod dry weight of genotypes between the first and the last sampling dates was highest at the dry site year Goodale 2003 and lowest at the wet site-year Goodale 2004. The early flowering genotypes 298T-9 and 272-2 had relatively high pod dry weight at the first one or two sampling dates, but were surpassed by high yielding genotypes like CDC Frontier and CDC Anna at later dates of sampling.

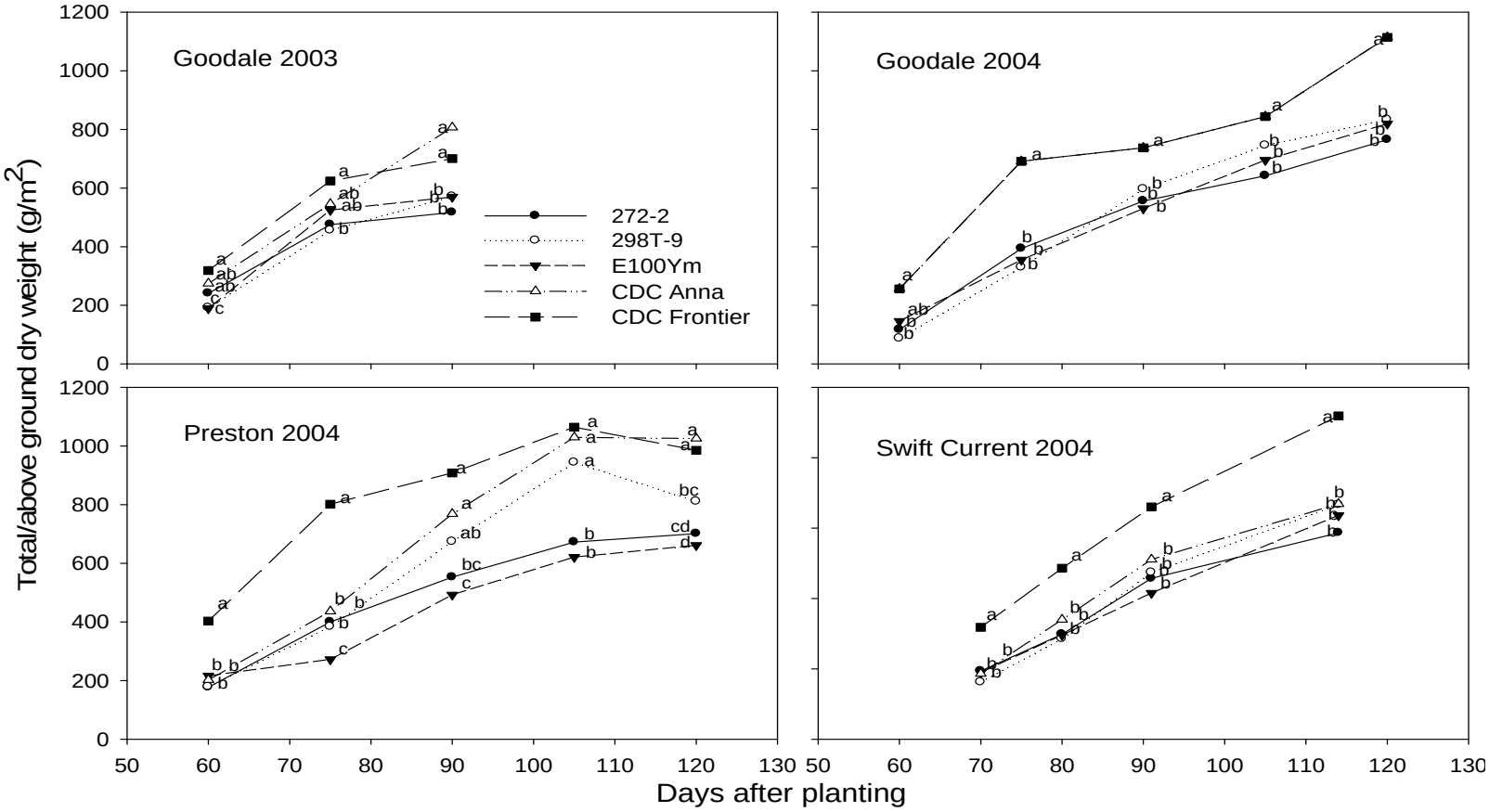

Fig. 6.1. Patterns of post-flowering total dry matter accumulation in five chickpea genotypes at four site-years in Saskatchewan, Canada. Means followed by the same letter on the same date are not statistically significant at $P \leq 0.05$.

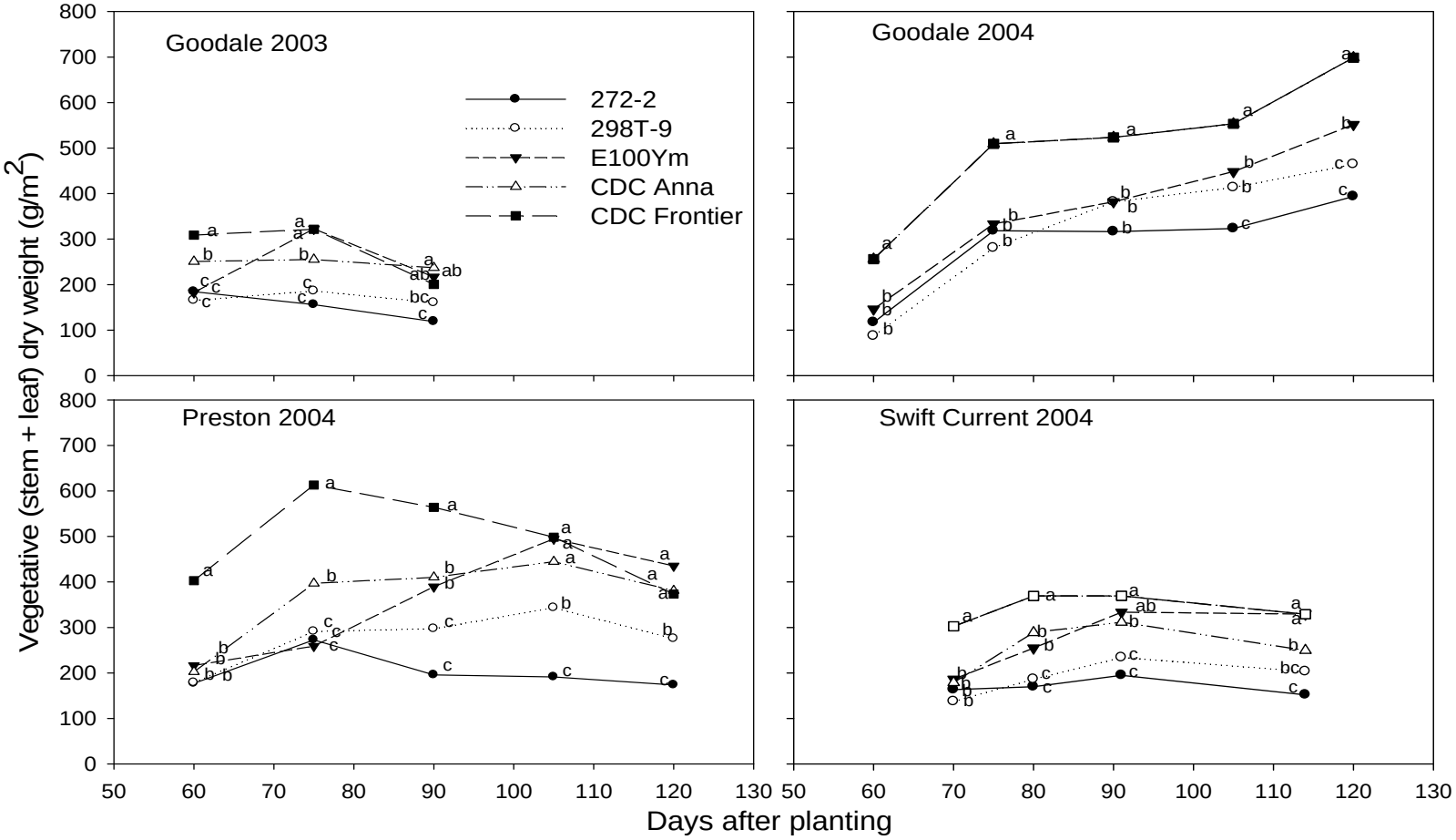

Fig. 6.2. Patterns of post-flowering vegetative (stem + leaf) dry matter accumulation in five chickpea genotypes at four site-years in Saskatchewan, Canada. Means followed by the same letter on the same date are not statistically significant at $P \leq 0.05$.

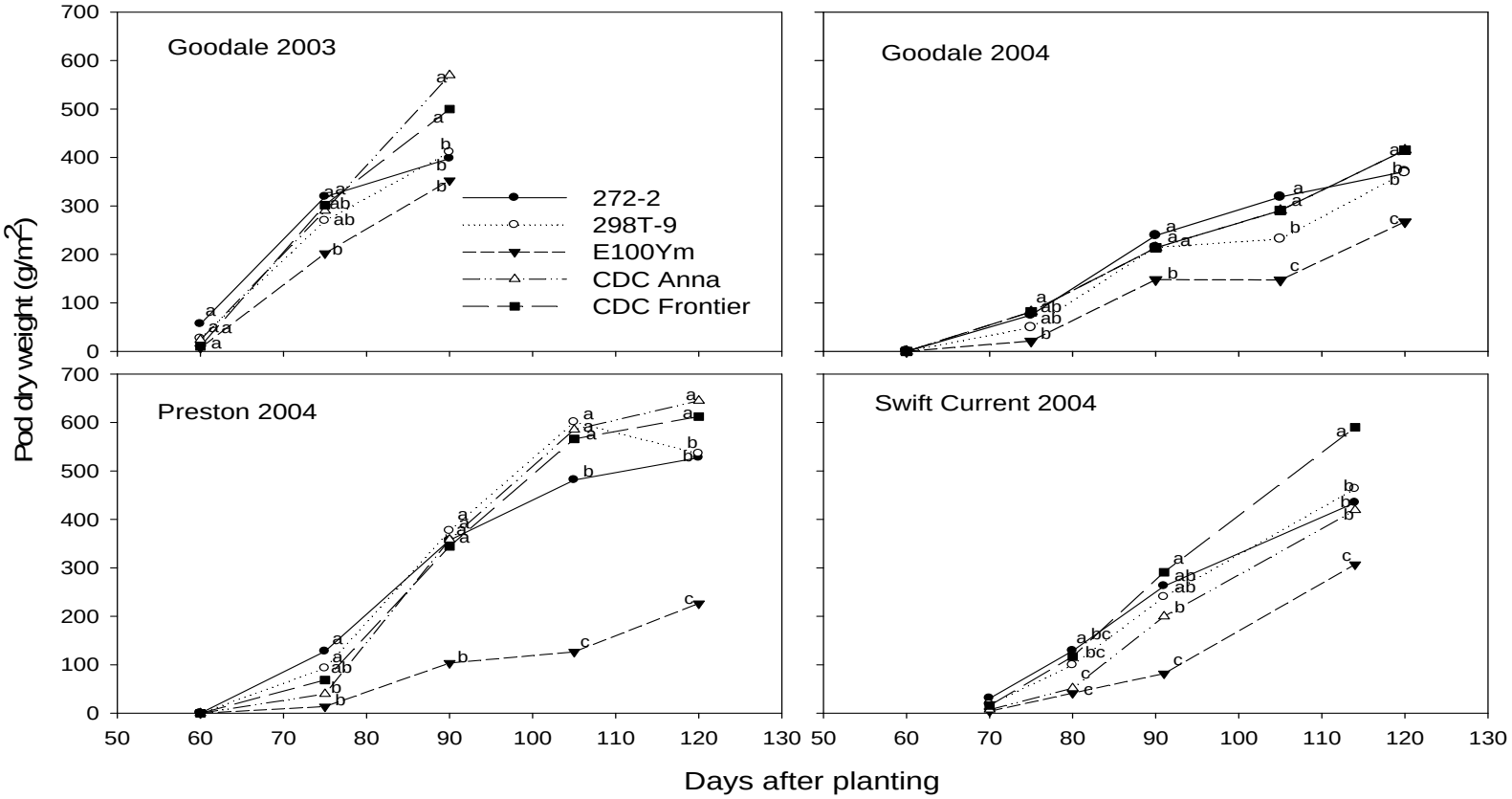

Fig. 6.3. Patterns of pod dry matter accumulation in five chickpea genotypes grown at four site-years in Saskatchewan, Canada. Means followed by the same letter on the same date are not statistically significant at $P \leq 0.05$.

6.3.4 Dry matter partitioning and maturity duration

There were systematic differences among genotypes in pod harvest index at the last sampling date as well as in the dry matter partitioning coefficient to pods, in parallel with their differences in maturity duration (Tables 6.4 and 6.5). In fact, plants have dropped most of their leaves at this sampling date and the pod harvest index figures were a bit exaggerated. Both pod harvest index and dry matter partitioning coefficient to pods were consistently high for the earliest maturing genotype 272-2. The dry matter partitioning coefficient to pods was also relatively high for CDC Frontier, which was late to flower but matured almost at the same time as the earlier flowering genotype 298T-9. Conversely, this coefficient was consistently low for E100Ym at all site-years, whose progress toward maturity was slow and incomplete at some site-years.

Pearson correlation analysis revealed negative associations between days to maturity and pod harvest index as well as between days to maturity and dry matter partitioning coefficient to pods at Goodale 2003 and Swift Current 2004, where complete maturity data is available (Table 6.6). Also, dry matter partitioning coefficient to pods was positively associated with pod harvest index, suggesting that a more efficient partitioning of dry matter to pods has increased pod harvest index and subsequently reduced time to maturity.

Table 6.4. Pod harvest index (%) at 90 days after seeding in 2003 and at 120 days after seeding in 2004 for five chickpea genotypes grown at four site-years in Saskatchewan.

Genotype	*Goodale 2003*	*Goodale 2004*	*Preston 2004*	*Swift Current 2004*	*Mean*
272-2	68.8	43.3	61.2	59.4	58.2
298T-9	65.8	40.7	54.0	55.7	54.0
CDC Anna	66.3	-	54.6	52.4	-
CDC Frontier	66.3	36.3	53.6	54.9	52.8
E100Ym	58.1	32.9	33.9	42.0	41.7
Mean	65.1	38.3	51.5	52.9	-
$LSD_{(0.05)}$	2.1	2.4	3.4	2.8	-
CV (%)	2.8	3.2	4.2	3.1	-

Dash shows that observation was missing.

Table 6.5. Estimates of dry matter partitioning coefficient to pods for five chickpea genotypes grown at four site-years in Saskatchewan.

Genotype	*Goodale 2003*	*Goodale 2004*	*Preston 2004*	*Swift Current 2004*
272-2	1.20 (0.10)	0.61 (0.09)	1.04 (0.11)	1.00 (0.02)
298T-9	0.99 (0.07)	0.52 (0.07)	0.84 (0.06)	0.88 (0.08)
E100Ym	0.78 (0.28)	0.43 (0.06)	0.43 (0.08)	0.68 (0.12)
CDC Anna	1.02 (0.03)	-	0.80(0.10)	0.84 (0.17)
CDC Frontier	1.19 (0.27)	0.51 (0.12)	1.00 (0.21)	0.98 (0.08)

Dash shows that observation was missing.

Values in parentheses are standard errors.

Table 6.6. Pearson correlation coefficients among pod dry weight, pod harvest index, dry matter partitioning coefficient to pods, and days to maturity at Goodale in 2003 (above diagonal) and Swift Current in 2004 (below diagonal).

Character	*PDW*	*PC*	*PHI*	*DM*
Pod dry weight (PDW)[z]	-	0.40	0.47	-0.20
Partitioning coefficient (PC)	0.80	-	0.90*	-0.91*
Pod harvest index (PHI)[z]	0.67	0.94*	-	-0.95**
Days to maturity (DM)	-0.60	-0.95*	-0.98**	-

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

[z] Determined at the last sampling date, 90 days after seeding at Goodale 2003 and 120 days after seeding at Swift Current 2004.

6.4 Discussion

Production experiences since the early 1990s revealed that chickpea crops often took longer to mature than what the season would typically allow in western Canada. In this study we attempted to determine whether timing of crop maturity was related to the patterns of post-flowering dry matter accumulation and partitioning to reproductive organs, so as to understand the specific changes required in growth strategies to allow timely maturity in this specific environment.

Significant differences were observed among genotypes in days to maturity, with about a two week gap between the earliest (272-2) and latest (E100Ym) genotypes at Goodale 2003 and Swift Current 2004. The benefit of early maturity was marked at Swift Current 2004 where over 90% of the seeds harvested were fully matured in 272-2 compared to less than 45% for CDC Anna, CDC Frontier and E100Ym (Table 6.3). Reproductive growth of 272-2 was less exposed to unfavorable weather conditions at the end of the growing season compared to the later maturing genotypes, such that the former genotype had less shriveled unfilled green seeds. For this reason, 272-2 had a relatively high yield at both Goodale 2003 and Swift Current 2004. This result is in agreement with the suggestion of Summerfield and Roberts (1988) that ensuring the maturity duration matched well the length of the favorable growing season is the most important step towards maximizing yield of chickpea.

Total dry matter showed an increasing trend over sampling dates, but the increase was at a decreasing rate beginning in mid-season. Since chickpea is a highly indeterminate species, availability of moisture encouraged continued growth and more dry matter accumulated during podding and grain filling stages, particularly at the wet

site-years. However, differences were noticed among genotypes in this post-flowering total dry matter accumulation, as had been reported previously by Guhey and Trivedi (2001) and O'Toole et al. (2001). The late flowering genotype CDC Frontier was superior in total dry matter at the first sampling date and maintained that supremacy throughout at most site-years. Being delayed in the onset of flowering, this genotype had more time for vegetative growth and a greater total dry matter accumulation. Similarly, Ellis et al. (2000) reported that late flowering (i.e. photoperiod sensitive) alleles in soybean have increased biomass accumulation under long day conditions.

In this study, the maximum total dry matter content of genotypes was not related to their differences in maturity duration, i.e. earlier maturing genotypes did not necessarily have a smaller maximum total dry matter content or vice versa. Bange and Milroy (2000) also did not observe difference between early and late maturing cotton genotypes in total dry matter. Asumadu et al. (1998) reported that the variation in the total dry matter accumulation was not solely a consequence of crop duration, and that mean crop growth rate was also an important contributor to the total dry matter. This implies that the adequate biomass production necessary to ensure optimal seed yield can be attained within shorter duration genotypes through a higher crop growth rate. Genetic variation in crop growth rate has been previously reported as a more important source of yield variation in chickpea than the variation in crop duration (Williams and Saxena, 1991).

For the genotypes used in this study, the vegetative dry matter accumulation tended to decline some time after flowering except at the cool and wet site-year of Goodale in 2004 (Fig. 6.2). This decline in vegetative dry matter was mainly due to

leaf senescence, which seemingly exceeded the rate of emergence of new leaves. In soybean, the decline in dry matter accumulation was consistent with the onset of leaf senescence and coincided with the decline in leaf area index (Pedersen and Lauer, 2004). The decline in vegetative dry matter accumulation started later for the late maturing genotype E100Ym at all site-years. On the other hand, the early maturing genotype 272-2 had significantly smaller vegetative dry matter accumulation during the latter part of the growth period, despite its comparable total dry matter production with genotypes 298T-9 and E100Ym. Shamsuzzaman et al. (2002) also reported that the more determinate early maturing chickpea genotype 'Hypersola' had significantly lower stem and leaf dry weight as compared to a genetically related long duration genotype during the last few weeks of its growth. It follows that there was a continued assimilation and increase in total dry matter, but the current assimilate was mostly partitioned to pods for genotype 272-2. Apparently, 272-2 was superior in dry matter partitioning coefficient to pods and this genotype also had a high pod harvest index at the last sampling date (Tables 6.4 and 6.5).

There were systematic differences among genotypes in dry matter partitioning coefficient to pods and pod harvest index, in parallel with their differences in maturity duration. Moreover, both dry matter partitioning coefficient to pods and pod harvest index were inversely related to days to maturity. This likely indicates that assimilate partitioning in ways that provide optimal proportion of pod dry matter is important for achieving early maturity in chickpea in western Canada. Detailed investigation into the relationship of timing of crop maturity with dry matter partitioning in cotton also showed that the key trait determining maturity was the preferential partitioning of dry

matter to pods (Pace et al., 1999). This result is consistent with the widely accepted hypothesis that early maturity is associated with high harvest index (Wallace, 1985).

It is apparent from these results that a more determinate nature, whereby dry matter is mainly partitioned to pods shortly after the onset of reproductive growth, would be useful to attain the extra early maturity characteristics desired in the western Canadian environment. When the reproductive sink uses the available assimilate supply, production of stem and leaves would cease, thus preventing the production of new podding sites (Hearn, 1972). In this case, assimilates are partitioned to pods, rather than continued vegetative growth and the production of late pods which are unlikely to reach full maturity (Whitehead et al., 2000). Such a more efficient partitioning of dry matter to pods along with the early flowering and podding habit needs to be targeted in cultivar development in chickpea in western Canada. However, the desired modifications should allow the flexibility to exploit any mid-season rainfall and maximize yield in drier seasons. In other words, complete determinacy may not always be beneficial in this environment, which in some cases experiences drought conditions as in 2003. Complete determinacy would likely reduce plant height and leaf area and limit the potential for biomass production and seed yield in drier years and at specific resource limited localities in the semi-arid region in the Prairies.

Grain yield is a function of the number of seeds produced per unit area and the average weight of the individual seeds (Shibles et al., 1975 cf Bruening and Egli, 1999). Seed number and weight are related to the availability of assimilate to the reproductive organs during flowering and fruit set, and prioritized partitioning of dry matter to reproductive parts will increase both of these yield components and ultimately seed

yield (Heitholt et al., 1985). Beaver and Cooper (1982) found that an early soybean genotype Corsoy produced seed yield as great as or greater than the full-season genotype Williams due to its superior rates of seed dry weight accumulation in central Illinois. Therefore, selection for more determinate genotypes in which the flowering period is condensed and the reproductive sink uses the majority of the post-flowering assimilate supply could improve earliness of crop maturity as well as seed yield in the short growing season of western Canada.

7. General Discussion and Conclusions

7.1 Inducing earliness in chickpea: key genetic traits and physiological mechanisms

In sharp contrast to many other growing environments, the maturation phase of chickpea coincides with declining temperatures and often wet conditions from August to October in the short-season temperate environment of western Canada. These wet and cool conditions exacerbate the indeterminate nature of the crop and delays maturity. In this environment, the chickpea crop is often exposed to frost damage resulting in reduced yield and quality. Genetic variability in duration of crop maturity was low in chickpea (Chapter 5), hampering progress in development of early maturing cultivars for this environment. It was hypothesized that earliness of crop maturity could be induced through short internode, double podding and early flowering. The use of similar key strategic genetic traits in plant breeding programs have in some cases brought about major achievements; for example, the semi-dwarf habit in wheat and rice (Athwal, 1971) and determinate/semi-determinate habit in soybean (Bernard, 1972). The effective coordinated action of the genes for short internode, double podding and early flowering would reduce the long season requirement of chickpea and subsequently minimize production risk.

7.1.1 Effect of short internode on maturity

In agreement with the finding of Sandhu et al. (1990), the short internode trait in the donor parent E100Ym was controlled by a single recessive gene. The presence of homozygous recessive alleles (*ptpt*) reduced internode length by half, from about two centimeters in normal plants to less than one centimeter in the mutant type, resulting in phenotypically distinct dwarf plants. However, a shorter plant height brought by this short internode allele (*pt*) had an undesirable effect on maturity duration, in that all the segregants in this phenotypic class were extremely late to mature. Field studies also showed that the parent E100Ym was late to mature compared to the known medium-late maturing cultivars CDC Anna and CDC Frontier.

The negative effect of the short internode trait on maturity may be attributed to the pleiotropic action of the allele as previously reported by Sandhu et al. (1990). The short internode allele is likely involved in gibberellin metabolism, which affected other characters such as leaf size and color, flowering, and pod development and then crop maturity. Like the known gibberellin mutant alleles *le, lh, ls* and *na* in pea (Reid, 1986; Reid and Ross, 1993), the *pt* allele in this population had a range of minor effects including reduction in leaf size and a darkening in leaf color together with the reduction in internode length. Physiological study revealed that E100Ym had slow growth and low efficiency of dry matter partitioning to the pods.

The short internode trait from a different allele may still be useful to induce early maturity in chickpea. At least two other dwarf mutants have been reported in chickpea (Singh and Dahiya, 1974; Shamsuzzaman et al., 2002). Short internode could help to reduce excessive canopy development, which is a main factor for delayed

maturity in chickpea in wet seasons in western Canada. In crops such as wheat and rice, dwarfing genes have been used to increase lodging resistance and harvest index and to contribute to early maturity (Athwal, 1971). Also, a more compact canopy would allow an increase in population density and provide an opportunity to maximize grain yield.

7.1.2 Effect of double podding on maturity

Chickpea typically produces one pod per peduncle, but a limited number of accessions in the chickpea germplasm produce two pods per peduncle at some reproductive nodes (Pundir et al., 1988; Srinivasan et al., 2005). A breeding line 272-2, which was derived from a cross with the known double podding accession JG 62, was used as the donor parent of the double podding trait for this study. The double podding population 272-2/CDC Anna segregated into 3 single podding : 1 double podding lines ratio at F_2, confirming the single recessive gene (*ss*) inheritance hypothesis for double podding (Kumar et al., 2000). It implies that the double podding trait can easily be incorporated into the desired genetic backgrounds.

Results of this study showed that the *s* allele had variable expressivity, determined as the percentage of the double podding nodes to the total podding nodes. This ranged from 0─34% in the F_2 population. Some lines had two flowers per peduncle, but only a single pod was fully developed. This was scored as 0% expressivity of double podding. Expressivity of double podding was consistently higher over generations in some lines than the donor parent 272-2. Kumar et al. (2000) also observed variable expressivity of double podding that ranged from 0.1─33% in the JG

62 x ICCV 2 recombinant inbred lines of chickpea. But, favorable genetic background for high expressivity of double podding is not fully understood.

When sufficiently expressed (i.e. > 15% of podding nodes bearing double pods), the double podding trait significantly reduced the duration of crop maturity. The best double podding lines, were about one week earlier than their single podding counterparts and other check varieties. This result implies that double podding is beneficial for earliness of crop maturity in genetic backgrounds and environments that allow high expressivity of this trait. Rubio et al. (2004) reported that the double podding allele conferred greater yield stability than the single podding allele in the Mediterranean region. The effect of double podding trait on yield stability may be attributed to its positive contribution to early maturity.

Growth analysis showed that the double podding genotype 272-2 partitioned a relatively higher proportion of dry matter to pods during the reproductive period and had high pod harvest index compared to other genotypes of a single podding habit. Thus, double podding resulted in a larger sink. This finding is in agreement with the nutritional hypothesis that when the reproductive sink monopolizes the available assimilate supply, production of stem and leaves would cease, thus hastening grain filling and finally leading to earlier crop maturity (Bange and Milroy, 2004).

7.1.3 Effects of early flowering on maturity

The genes for time to flowering are known to also pleiotropically influence the maturity duration in many crop plants (Wallace, 1985; Wallace et al., 1993). The present study showed that time to flowering influenced maturity duration mainly

through its effect on timing of the beginning of maturity of lower pods. Time to flowering was positively associated with days to maturity, and partial path analysis revealed that the relation of days to flowering with days to maturity was indirect, mainly via days to first pod maturity. Further, days to flowering explained about 32% of the variation in days to first pod maturity. Early start of maturity of lower pods would be beneficial to progress towards full crop maturity before the occurrence of fall frost.

A substantial variation in flowering time is available among chickpea germplasm (Pundir et al., 1988) as a result of genotypic response to temperature, photoperiod and their interactions with the environment. A further reduction in time to flowering in chickpea may be achieved in western Canada by the introduction of allelic variations for day length and temperature responses derived from alien germplasm sources, such that an extra early flowering and maturity habit will enable the crop to escape frost damage.

In summary, the present study showed that early flowering and double podding traits would positively contribute to earliness of crop maturity. Both of these traits are under simple genetic control and can easily be incorporated into the desired genetic backgrounds or could easily be combined into a single genotype (Sheldrake et al., 1978; Kumar et al., 2000; Or et al., 1999; Kumar and van Rheenen, 2000; Anbessa et al., 2006). Pyramiding the genes for these and other strategic genetic traits such as early vigor, basal branching, higher partitioning efficiency to pods, etc. should significantly reduce the long season requirement of this crop and subsequently minimize the frost risk associated with chickpea production in western Canada. If such

extra short-duration genotypes become available for cultivation in this environment, chickpea productivity will increase and stabilize at a higher level contributing to substantial growth of the industry.

7.2 Genetics of Earliness Traits in Chickpea

7.2.1 Inheritance of time to flowering

Time to flowering has an adaptive significance and also has a favorable effect on grain yield (Kumar and Abbo, 2001). Information on its inheritance mechanism is required to formulate the most efficient breeding strategy for improvement of time to flowering in chickpea in the short-season temperate environment in western Canada. Or et al. (1999) and Kumar and van Rheneen (2000) each reported the presence of one major gene for time to flowering in chickpea, but it is not known whether the two major genes reported by these authors are the same or not. In the populations used for this study, time to flowering was governed by two major genes plus polygenes. The two major genes controlled the majority of the variation (> 65%) for this trait. Late flowering was dominant over early flowering for both major genes with digenic interaction between them, mainly an additive x additive type. This implies that the backcrossing or single seed descent breeding methods could effectively be deployed to reduce time to flowering in chickpea.

Although no allelism test was made, pedigree information of the parents for our populations indicate that one of the alleles reported herein is likely the *efl-1* allele from ICCV 2 previously reported by Kumar and van Rheenen (2000). ICCV 96029, which

was developed from a cross between ICCV 2 and ICCV 93929 (Kumar and Rao, 2001), was an indirect source of early flowering alleles for our populations. However, ICCV 96029 was about one week earlier than ICCV 2 at ICRISAT, Patancheru, India (Kumar and Rao, 2001). This genotype likely has an additional allele for early flowering, which is strongly supported by our finding.

Physiological study revealed that time to flowering is a function of temperature and photoperiod in chickpea (Roberts et al., 1985). The two major genes may each determine response to either factor. Snape et al. (2001) reported that different major genes control temperature and photoperiod effects on time to flowering, and that 'earliness per se' is determined by polygenic background in wheat. However, it is possible that both flowering genes in chickpea reported herein may respond to the same environmental factor. In pea, response to photoperiod alone is determined by a complementary three gene system (Arumingtyas and Murfet, 1994).

7.2.2 Heritability and predicted gain for some earliness traits

Genetic analysis of ten quantitative traits related to crop duration in chickpea was carried out using early generation segregating populations (F_2─F_4 generations) as well as recombinant inbred lines. These included days to flowering, days to first podding, pod establishment period, days to first pod maturity, pod filling period, reproductive period, number of nodes to first pod, height to the first pod, height at flowering, and increase in height after flowering. The results showed that some of the key phenological traits including days to flowering, days to first podding, days to first pod maturity, percent pod maturity, reproductive period, and days to maturity are

mainly under additive genetic variance. Kumar et al. (1999) also observed that days to flowering, days to first podding and days to maturity were mainly under the control of additive genetic variance. Moderately high heritability estimate of 46% was obtained for days to flowering and days to maturity.

Since chickpea is an inbreeding species and genotypes are inbred lines, traits which were predominantly under additive genetic variance such as days to flowering, days to first podding, days to first pod maturity and percent pod maturity at four months after seeding are important for improvement. These could be manipulated separately in the breeding process to reduce the overall crop duration. Selection for each trait is beneficial for early maturity, but additional genetic gain is possible by combining all the traits into a single genotype. The recurrent selection scheme that allows the accumulation of favorable alleles for all important components of crop duration through repeated crossing may lead to a greater genetic gain from selection.

Predicted gain from selection for the different earliness traits was generally low owing to small genetic variability detected within the segregating populations. Previous studies also concluded that genetic variability was low in chickpea (eg. Ahmad and Slinkard, 1992). If substantial improvement is to be made it is important that the genetic variability in the segregating populations be increased through wide and complex crosses involving gene introgression from across desi and kabuli types and from wild relatives. Singh and Ocampo (1997) reported broad variations among the F_2 and F_3 lines from a cross between *Cicer arietinum* with its primary wild progenitor, *Cicer reticulatum*. Maynez et al. (1993) also showed that greater genetic distance between parental lines resulted in higher genetic variance among the progeny in

economically important traits in chickpea. Breeders could therefore better tailor earliness of crop maturity in this environment by including genetically divergent parents in the crossing scheme.

7.3 Future Research

Owing to the short history of chickpea research in western Canada, basic studies pertaining to earliness of crop maturity are minimal thus far. The problem of late maturity in this environment is on the other hand unique in nature and information available elsewhere may not be directly applicable. If substantial improvement is to be made in early maturity in chickpea in western Canada, basic studies need to continue to build upon the information generated in this study.

This study showed that time to flowering was determined by at least two complementary major genes in chickpea. The reaction of these genes to photoperiod and temperature need to be elucidated for full understanding of the genetic system required for the western Canadian environment. Further study may also reveal other alleles from different genetic backgrounds for time to flowering, which may help to further reduce time to flowering. At least six loci governing the variation in time to flowering were reported in soybean (Bernard, 1971; Buzzell, 1971; McBlain and Bernard, 1987; Bonato and Vello, 1999).

The double podding trait had substantial effect on maturity duration, but this was evident only under conditions in which the character was sufficiently expressed. Certain lines showed consistently higher expressivity of double podding than others.

Favorable genetic backgrounds for high expressivity of double podding need to be determined so that the benefits of this trait may be maximized. It is also important to determine whether all the double podding chickpea accessions carry the same allele or not. If different, these alleles could be combined for higher expressivity of double podding.

Identification and use of strategic genetic traits leading to greater physiological determinacy are important for the development of early maturing chickpea cultivars for this environment. Although the *pt* allele for the short internode trait had undesirable effects on maturity, the short internode trait from other alleles could still be used to reduce excessive canopy development. The highly indeterminate nature and subsequent excessive canopy development in wet seasons, is a main factor for delayed maturity in chickpea in western Canada. Crop canopy modification through a more basal branching habit should also be sought. Genes that affect reduction in apical dominance could ultimately lead to a more basal branching habit. Basal branches, being formed early during crop growth, may enable the chickpea plant to have a more synchronized production of flowers and pods, and maturity of these pods.

Induced mutation could be used as an alternative strategy to develop an improved chickpea plant type for this environment. Mutation activities could increase variability for earliness parameters, which could be used in breeding programs. Mutants with early flowering/maturity habit, determinate growth habit could be developed through this approach. Maiti and Zavala-Garcia (2001) described various useful mutants in chickpea including bushy plant type, short internode, double pod and multiseed character, and mutants of leaf types and arrangements. 'Hypersola', a more

determinate chickpea genotype was also developed through mutation (Shamsuzzaman et al., 2002). Mutation resulting in allelic variability is also important for genetic studies.

As indicated in chapters three through six, some herbicides were used for weed control in the experimental plots. However, chickpea may be sensitive to various herbicides. Herbicide residue in the soil and/or incorrect application conditions of herbicides could cause crop injury and reduce the rate of crop growth, potentially resulting in delayed flowering and maturity. It is important that the effect of various herbicides on crop maturity be critically assessed to minimize phytotoxicity.

In conclusion, the level of improvement required in reducing the crop duration in chickpea in western Canada is large and could be attained in the long run. Significant reduction in crop duration could be made by adopting short term strategies of incorporating important genetic traits into genotypes allowing incremental progress. This approach will subsequently lead to a better conceptualization of plant ideotype that is appropriate for the environment and form the basis for developing well-adapted genotypes for western Canada through breeding.

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Appendix I. On Improving Crossing Success in Chickpea

Artificial hybridization in chickpea, operated independently for each small floret, is known to be very tedious. Superimposed upon this constraint is the rate of crossing success which is critically low in this crop, about 10% or less in many cases (Bejiga and Tessema, 1981). In both domestic and naturally occurring plants, there is evidence that crossing success may be influenced by the environment in which a plant grows and by parental identity (Pittman and Levin, 1989). Identification of parental traits which could help to overcome this problem, even only to some extent, would benefit chickpea improvement efforts significantly. This study was initiated to determine the influence of variable male and female parents on crossing success in chickpea.

Five divergent parental genotypes chosen for this study were systematically intercrossed, including reciprocal crosses, in growth chambers at the University of Saskatchewan, Saskatoon, Canada (Appendix Table 1). Five plants of an individual parental genotype were grown in each 30 cm diameter pot filled with Redi-Earth soil (W.R. Grace and Co., ON, Canada) for crossing. Crossing was repeated four times by planting the crossing block on different dates.

Emasculation (i.e. removal of undehisced anthers) and subsequent hand pollination were conducted at 'half open flower' stage (Dahiya, 1974). Label tags were tied to the peduncle and subtending leaf together for each hand pollinated flower. The

same person did all of the crossings. Hybrid pods were counted and harvested independently for each pot. Percent crossing success was then determined as the percentage of pollinated flowers which gave rise to successful hybrid pods. Leaves subtending flowers at the pollination stage were randomly picked to determine specific leaf area and specific leaf weight at that stage following the method used by Anbessa and Bejiga (2002).

Twenty-five randomly picked F_1 seeds from each cross were planted and evaluated along with the parents in the greenhouse. The hybrid nature of the F_1 plants was confirmed using morphophenological traits in which the parental genotypes differed. Pod volume and seed sizes of the subsequent F_2 seeds were also analyzed to see if there were differences between reciprocal crosses for these traits.

Analysis of variance revealed highly significant ($P < 0.01$) differences among crosses in total number of hybrid pod set and percent crossing success. Further comparison between the male and female parents revealed that the female parent was the determining factor. The percent crossing success ranged from 8.2─42.7, depending upon the female parent used (Appendix Fig. 1). Maherchandani (1979) also found significant differences in hybrid pod set only among female parents in reciprocal crosses of five genotypes. This implies that parental identity influences crossing success in chickpea.

Percent crossing success was highest when the small seed size genotype 272-2 was used as the female parent (Appendix Fig. 1). Further, both mean pod set pot^{-1} and percent crossing success were strongly and negatively associated with 100 seed weight of the female parent. This may in part be attributed to negative compensation between

seed size and seed number (Board et al., 1999). It is suggested that parents with smaller seed size should be used as the female parent in chickpea crosses, unless the nature of the study forces one to set otherwise.

Large seed size is one of the major objectives of chickpea breeding, especially in the Kabuli market class. In this study, there was no difference between reciprocal crosses in pod volume and mean seed weight of F_2 seeds. Therefore, progress in the improvement of seed size will not be affected if the smaller seeded parent is used as female parent for hybridization as suggested above.

It was observed that leaves subtending flowers at the stage of pollination were much smaller than mature leaves of the same plant, especially on the upper reproductive nodes. Brown (1984) indicated that indeterminate species continue to form leaves while fruiting, but the rate of leaf formation is lower than the rate of emergence of flower buds. Thus, as more reproductive nodes form, flowers open nearer to the apical bud, where leaves are newly formed.

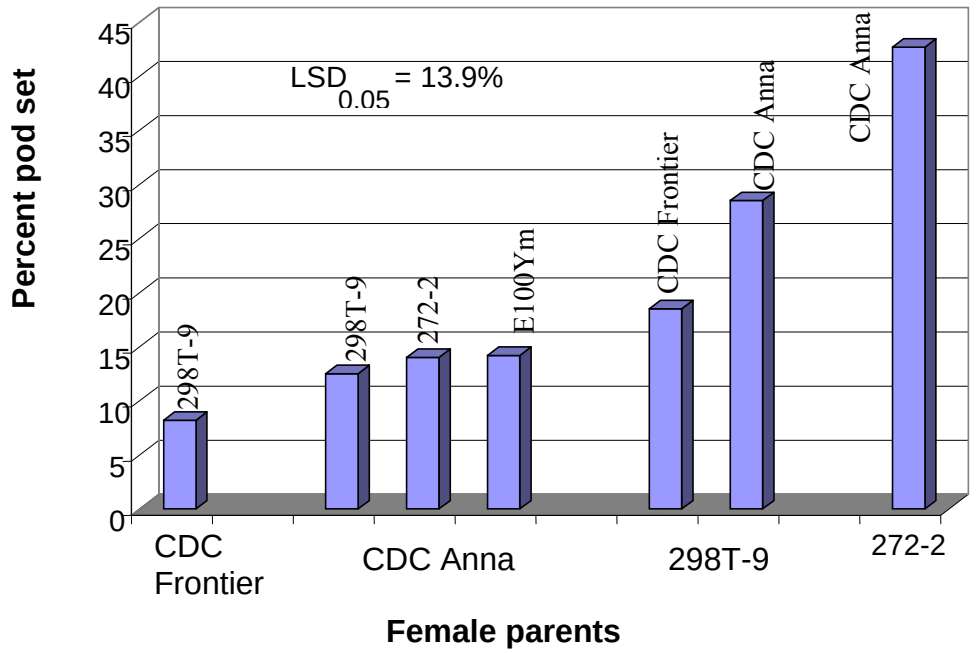
The female parents used in this experiment had substantial differences both in specific leaf area and specific leaf weight of the leaves subtending flowers. Mean pod set $pot^{-1}$and percent crossing success increased sharply with the increase in area of the leaf subtending flowers in female parents. Pearson correlation coefficient of specific leaf area and mean pod set was 0.987 ($P < 0.01$) and it was 0.983 ($P < 0.02$) between specific leaf area and percent crossing success. This indicates that limited assimilate supply is partly responsible for failure of crosses to set seed. Pod or seed numbers are frequently modeled as a function of the assimilate supply from photosynthesis (Charles-Edwards, 1984). The overall photosynthate supply may not be limiting, but the

subtending leaf is yet growing and is a net importer, competing with the young pod for translocated assimilate from leaves below that region.

In conclusion, for better crossing success the parent with smaller seed size should be used as the female parent in chickpea crosses, unless the nature of the study forces one to set otherwise. Further, selective crossing to flowers with relatively larger subtending leaves, either due to the genetic nature of the mother plant or the position in the canopy, would improve the rate of success in chickpea crossing.

Appendix Table 1. Description of female parents used and crosses conducted.

Cross	Distinctive characters of the female parent
298T-9/CDC Anna 298T-9/CDC Frontier	Early flowering with medium seed size (20g/100 seeds)
272-2/CDC Anna	Double podding, early flowering with small seed size (14g/100 seeds)
CDC Anna/298T-9 CDC Anna/272-2 CDC Anna/E100Ym	Commercial desi type variety with medium-late flowering and medium seed size (~24g/100 seeds)
CDC Frontier/298T-9	Commercial kabuli type variety with late flowering and large seed size (38g/100 seeds)



Appendix Fig. 1. Percent pod set as affected by female parent in some chickpea crosses. Male parents indicated on top of the respective bar.