# Assessing genetic variation in growth and development of potato

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# Assessing genetic variation in growth and development of potato

**Muhammad Sohail Khan**

**Thesis**

submitted in fulfilment of the requirements for the degree of the doctor
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# Abstract

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Due to increasing food demand and changing diets potato (*Solanum tuberosum* L.) is becoming a subsistence crop in many regions. However, the agronomy and whole crop physiology of tuber yield production is extremely complex, due to genotype and environment specific effects on crop physiological and morphological characteristics. Such intrinsic complexities complicate the manipulation of yield determining traits and make their prediction a challenging task. The genetic improvement of tuber yield can be understood more mechanistically by investigating and interpreting the relationships between the main attributes of crop growth.

This thesis aims to develop an approach to quantify the yield of individual genotypes and to estimate parameters which may reveal the effects of genetic and environmental factors on the important plant processes controlling tuber yield variation among a large set of F1 (SH83-92-488 × RH89-039-16) genotypes of potato and a set of standard cultivars covering a wide range of maturity types.

It first presents a model approach to analyse the time course of canopy cover and tuber bulking during the entire crop cycle as a function of thermal time in terms of large number of physiological component traits and explain their inter-relationships and impact on crop maturity and tuber yield production across six contrasting field experiments. The results indicated that the length of the canopy build-up phase ($D_{P1}$) was conservative with respect to genotype's maturity type, but the duration of maximum canopy cover ($D_{P2}$) and the decline phase ($D_{P3}$) varied greatly, with later genotypes having longer $D_{P2}$ and $D_{P3}$ and thus a higher area under whole green canopy curve ($A_{sum}$). Values of tuber bulking rate ($c_m$) were highest for early maturing genotypes followed by mid-late and then late genotypes. Late maturing genotypes had longest effective duration of tuber bulking ($ED$) followed by mid-late and early genotypes. As a result tuber yield ($w_{max}$) was higher in late genotypes than in early genotypes. The radiation use efficiency (RUE) values were highest for early maturing genotypes followed by mid-late and late genotypes whereas nitrogen (N) use efficiency (NUE) was highest in late maturing genotypes followed by mid-early and early genotypes.

High genetic variability and high heritability for most of these traits were found. Results indicated that increased tuber yield by indirect selection for optimal combination of important physiological traits can be achieved. While using these traits as a criterion for selection, the causal physiological relationships and trade-offs must be considered simultaneously.

Our molecular dissection of traits determining the dynamics of canopy cover, tuber

bulking, and resource (radiation, nitrogen) use efficiencies identified several QTLs, the mapping position of each identified QTL, the interaction of QTL with environment (QTL×E) and the magnitude of the QTL effect in explaining genetic variance in both SH and RH parental genomes. The QTL results indicated that one particular chromosomal position at 18.2 cM on paternal (RH) linkage group V was tightly linked to the genotype's earliness and controlling nearly all the traits and explaining the phenotypic variance by up to 79%. This suggested the pleiotropic nature of the QTL for most of the traits determining crop maturity and tuber yields. A number of QTLs for traits were not detected when tuber yield *per se* was subjected to QTL analysis. The phenotypic variance explained by the QTLs for tuber yield *per se* was also lower than for other traits.

The physiological and quantitative knowledge gained was used to evaluate the conventional system of maturity type and to quantify and re-define the concept of maturity type on a physiological basis for a large set of genotypes. Four new physiological based maturity criteria were developed based on four canopy cover and tuber bulking traits. Physiological maturity type criteria tended to define maturity classes less ambiguously and were easily and clearly interpretable compared to the conventionally used method of defining maturity.

The capability of an ecophysiological model 'GECROS' was tested to analyse differences in tuber yield of potato. The model yielded a reasonably good prediction of differences in tuber yield across environments and across genotypes. Model analysis identified the genotypic key-parameters affecting tuber yield production and $N_{max}$ (i.e. total crop N uptake) contributed most to the determination of tuber yield. The results concluded that genotypes with higher $N_{max}$ and lower tuber N content exhibited higher tuber dry matter yield. Further analysis of the genotypic parameters should be performed in conjunction with molecular markers in order to determine their genetic control and to proceed towards QTL-based crop modelling approach.

This thesis identified the dominant component traits mostly involved in the formation of a tuber yield and gave insight into the possibilities of genetically and physiologically manipulating the size or number of such traits. The information obtained should help in marker-assisted selection as well as in designing ideotypes for specific and/or diverse environments. However, to make significant contributions for breeding, there is a need for further research efforts to evaluate the combined physiological and genetic approach.

**Key words:** Potato (*Solanum tuberosum* L.), segregating population, canopy cover dynamics, tuber bulking dynamics, beta function, thermal time, components of variance, genotype-by-environment interaction (G×E), heritability, QTL mapping, QTL-by-environment (QTL×E) interaction, complex traits, ecophysiological crop model, GECROS, cultivar choice, maturity type, ideotype breeding, tuber yield.

*Dedicated to my beloved parents*
*&*
*highly esteemed supervisors*

# Contents

# Abbreviations

| | |
|---|---|
| $T_b$ | Base temperature (˚C) |
| $T_o$ | Optimum temperature (˚C) |
| $T_c$ | Ceiling temperature (˚C) |
| $t_{m1}$ | Inflexion point during canopy build-up phase (*td*) |
| $t_1$, $D_{P1}$ | Period from plant emergence to maximum canopy cover (moment and duration since emergence, respectively) (*td*) |
| $t_2$ | Onset of canopy cover senescence (*td*) |
| $t_e$ | Time of complete senescence of canopy cover or crop maturity (*td*) |
| $v_{max}$ | Maximum level of canopy cover (%) |
| $c_{m1}$ | Maximum canopy growth rate during build-up phase (% $td^{-1}$) |
| $c_1$ | Average canopy growth rate during build-up phase (% $td^{-1}$) |
| $c_3$ | Average canopy senescence rate during decline- phase (% $td^{-1}$) |
| $D_{P2}$ | Total duration of maximum canopy cover phase (*td*) |
| $D_{P3}$ | Total duration of canopy senescence phase (*td*) |
| $A_1$ | Area under canopy curve for $D_{P1}$ (*td %*) |
| $A_2$ | Area under canopy curve for $D_{P2}$ (*td %*) |
| $A_3$ | Area under canopy curve for $D_{P3}$ (*td %*) |
| $A_{sum}$ | Area under whole green canopy curve (*td %*) |
| $t_B$ | Onset of linear phase of tuber bulking (*td*) |
| $t_E$ | End of linear phase of tuber bulking (*td*) |
| *ED* | Total duration of tuber bulking (*td*) |
| $c_m$ | Rate of tuber bulking (g $td^{-1}$) |
| $w_{max}$ | Maximum tuber dry matter at crop maturity (g $m^{-2}$) |
| RUE | Radiation use efficiency (g DM $MJ^{-1}$) |
| NUE | Nitrogen use efficiency (g DM $g^{-1}$ N) |
| $m_V$ | Period from plant emergence to onset of tuber bulking (*td*) |
| $m_R$ | Duration between onset of tuber bulking and crop maturity (*td*) |
| $H_{max}$ | Maximum plant height (m) |
| $n_{SO}$ | Maximum tuber N concentration (g N $g^{-1}$ DM) |
| $N_{max}$ | Total crop N uptake at crop maturity (g N $m^{-2}$) |
| *td* | Thermal day |
| cM | centiMorgans |

# CHAPTER 1

# General introduction

**Increasing sustainable yield**

A major agricultural challenge facing the world today is providing sufficient food to meet the demands of a rapidly growing population. The goal of any plant breeding programme is the development of new, improved cultivars or breeding lines for particular target areas and to increase the sustainable yield and quality of crop plants to meet projected increases in global food demand (FAO, 1996). This normally involves manipulating complex traits associated with plant growth and development, usually in production environments that are highly variable and unpredictable.

Genetic improvement can be achieved by selecting directly for a primary trait (such as yield) in a target environment (Ceccarelli and Grando, 1996). This has been referred to as *empirical* or *traditional* breeding. Another - indirect way - is to select for a secondary trait(s) that is putatively related with a higher yield potential and/or to the improved behavior of the crop when grown in a particular environment. This is known as *analytical* or *physiological* breeding.

Over the past century, most of the progress in breeding in most crops species has been derived from empirical breeding, which has taken yield as the main trait for selection (Austin et al., 1989; Khush, 1987; Russell, 1993; Evans, 1993; Slafer et al., 1994). For instance, in cereals, yield increases have been possible through the gradual replacement of traditional tall cultivars by semi dwarf and fertiliser-responsive varieties with superior harvest indices. The term “Green Revolution” was coined to describe this process.

However, most agronomic traits are physiologically and genetically complex (Lark et al., 1995; Orf et al., 1999; Daniell and Dhingra, 2002; Stuber et al., 1999). For instance, yield is the outcome of many underlying morphological and physiological processes (Bezant et al., 1997). Furthermore, it is a quantitatively inherited trait under polygenic control, and characterised by low heritability and a high genotype-by-environment (G×E) interaction (Allard and Bradshaw, 1964; Jackson et al., 1996; Tardieu, 2003). Such intrinsic complexities complicate the manipulation of quantitative crop traits and make their prediction a challenging task. Therefore new approache(s) which could complement traditional with analytical selection methodologies to further improve crop yields and the overall efficiency of the breeding process are of considerable interest to plant breeders.

**Genomics based approaches**

Recent advances in agricultural genomics and marker-assisted selection have totally revolutionised and enhanced the plant breeding process (Somerville and Somerville, 1999; Yin et al., 1999a; Huang et al., 2002; Knight, 2003). The advent of DNA-based molecular markers (Botstein et al., 1980; Paterson et al., 1988) and new state of the art statistical methods (Lander and Botstein, 1989; Jansen, 1993; Jansen and Stam, 1994) have made it possible to localise polygenes controlling complex quantitative traits and study the effect of individual genes on the trait, which was difficult in classical quantitative genetics.

The acronym QTL stands for *Quantitative Trait Locus*, with plural QTLs, and has come to refer to a genomic region associated with a quantitative trait (Yin et al., 1999a). Numerous studies have been reported on identification of QTLs for various quantitative traits in humans, animals, and plants (Yin et al., 1999a). The increasing knowledge on QTLs for important agronomic traits can provide new avenues for the breeders to speed up the process of increasing crop yields (Morandini and Salamini, 2003).

Although QTL mapping technologies have allowed significant advances in crop genetic improvement, there still exist challenges to increase the yield potential of crops (Yin et al., 2003a). One major difficulty in the use of QTLs of traits is their instability across environments (Reymond et al., 2003) due to complex QTL-by-environment (QTL×E) interactions. For instance, Ribaut and Hoisington (1998) found 13 QTLs in a study of flowering dates of maize, but only three were common to three experiments with different levels of water deficit. Consequently, many QTLs can be only detected in a narrow range of environmental conditions (Zhou et al., 2007) and the classical genetic models built from QTL analysis have a correct predictive ability only in a limited range of conditions.

Popular QTL-analysis methods will have difficulties handling these complexities. Without increasing population sizes, limited reliability in QTL detection and estimation can be achieved (Kearsey and Farquhar, 1998). To overcome these bottle necks, support from other disciplines is required. There is an identified need to separate factors influencing a given phenotypic trait and shifting from highly integrated traits to more gene-related traits (Yin et al., 2002). Several studies have underlined the potential interest in building such a link (Hammer et al., 2002, 2006; Tardieu, 2003; Yin et al., 2004). Functional genomics, systems biology, and crop physiology can jointly improve genetic analysis and breeding efficiencies.

**Role of systems approaches in model based breeding**

There is increasing advocacy for the application of crop physiological knowledge and integrative modelling in breeding for complex traits (Campos et al., 2004; Edmeades

et al., 2004; Yin et al., 2004; Hammer et al., 2005). Crop modelling can play a significant part in system approaches by providing a powerful capability for phenotype prediction and yield scenario analysis (Hammer, 1998; Cooper et al., 2002; Hammer et al., 2004).

Crop growth models are simplified mathematical representations of the interacting biological and environmental components of the dynamic plant system. Ecophysiological crop growth models have been developed extensively during the last decades by integrating knowledge across many disciplines such as crop ecophysiology, micrometeorology, soil science, and computing technologies (Loomis et al., 1979; Ritchie, 1991; Boote et al., 1996; Bouman et al., 1996; McCown et al., 1996). These models have been conventionally used to predict the performance of given cultivars under various environmental conditions, and are now increasingly being used in breeding programmes (Aggarwal et al., 1997).

One of the main applications of ecophysiological crop growth models is their explanation of differences in yield potential of genotypes on the basis of individual physiological parameters (Kropff et al., 1995; Haverkort and Kooman, 1997). This is possible because their parameters can be used to mimic genetic characteristics of plants when crop growth models become more mechanistic and comprehensive (Boote et al., 1996). Values of these parameters are specific to each genotype and constant under a wide range of environmental conditions therefore are often referred to as *genetic coefficients* (Hoogenboom et al., 1997; Boote et al., 2001; Tardieu, 2003; Bannayan, 2007), reflecting the awareness that the variation of these parameters is under genetic control (Stam, 1996). These parameters could be therefore considered as quantitative traits and are amenable to further analysis (Yin et al., 2004; Quilot et al., 2005), e.g. for QTL mapping, and evaluating and designing ideotypes (Loomis et al., 1979; Kropff et al., 1995; Boote et al., 1996; Haverkort and Kooman, 1997; Yin et al., 2004; Yin and Struik, 2008).

Ecophysiological models can make it possible to explore the impact of new genotypes and the contribution of individual physiological traits on yield by simulating genotypes under any defined environmental scenarios as well as a range of management options (Stam, 1996; Bindraban, 1997; Hoogenboom et al., 1997; Asseng and Turner, 2007). Such models could help in understanding of G×E interaction and may speed up crop improvement for specific environments (Kropff and Goudriaan, 1994; Roberts et al., 1996; Boote et al., 2001; Slafer, 2003; Yin et al., 2004; Mayes et al., 2005) and to assist plant breeding to better quantify crop genotype-phenotype relationships (Yin et al., 2000a, 2004; Reymond et al., 2003; Hammer et al., 2006).

Improved phenotypic predictions via crop modelling result from their ability to

deal with the complex interactions among plant growth and development processes, environmental effects and genetic controls. This predictive capacity of the dynamic model could be used for favourably weighting more important QTLs during their selection in marker-assisted breeding programmes. Crop physiology using crop models therefore can also reinforce the QTL analysis of complex traits, thereby improving breeding efficiency and enhancing genetic design (Yin et al., 1999a,b, 2000a).

When QTL information is incorporated into crop models, the 'QTL-based crop models' could provide valuable insights into which combinations of alleles favour adaptation to specific environments, therefore should narrow down genotype–phenotype gaps. They can potentially be a powerful tool to resolve the phenomenon of G×E interaction and therefore overcome the limitation that QTL mapping cannot extend an experimental result of one environment to another environment condition (Messina et al., 2006). Based on recent studies (e.g. Reymond et al., 2003; Yin et al., 2005a; Gu et al., 2012), there is now increasing advocacy for *QTL-based* modelling approaches, i.e. linking crop modelling with QTL mapping for complex traits.

If crop physiology and genetics are combined judiciously, crop physiology and modelling research can reinforce the genetic analysis of complex traits and thereby can offer the possibilities of *model-based* breeding. Promoting this novel role of crop physiology, however, requires a new generation of crop models. Such models should have robust model architecture, numerical consistency, stability, and enhanced heuristics. Most importantly, crop models should include genotype-specific parameters for incorporating the latest findings offered by the rapid advances in functional genomics (Yin et al., 2004). Such models would greatly enhance our ability to translate short-time scale gene-level information to the crop performance in continuously changing field environments.

**GECROS: An improved state of the art ecophysiological model**

Recently, a state of the art ecophysiological crop growth model called GECROS (Genotype-by-Environment interaction on CROp growth Simulator), based on the above lines of thinking for improved model structure and input parameters, was developed by Yin and Van Laar (2005). GECROS uses new algorithms to summarise current knowledge of individual physiological processes and their interactions and feedback mechanisms. It attempts to model each sub-process at a consistent level of detail, so that no process is overemphasised or requires too many parameters and similarly no process is treated in a trivial manner, unless unavoidable because of lack of understanding. GECROS also tries to maintain a balance between robust model structure, high computational efficiency, and accurate model output. The model can

be used for examining responses of biomass and dry matter production in arable crops to both environmental and genotypic characteristics. In this study we explored the ability of GECROS to analyse differences in tuber yield in a set of varieties covering a wide range of maturity types and a well-adapted diploid F1 segregating population of potato (*Solanum tuberosum* L.).

**Potato: Origin and importance**

Potato (*Solanum tuberosum* L.) is an annual crop from the genus *Solanum* (family Solanaceae) (Khurana et al., 2003). The potato originates from the mountains of South America where it has been an important food crop for a long time (Rowe, 1993). In the 16$^{th}$ century the potato was introduced to Europe as a curiosity, first to Spain and then into England (Hawkes, 1990; Spooner et al., 2005). Gradually it became a major food crop, especially when varieties were selected which were adapted to long day conditions. In the 18$^{th}$ and 19$^{th}$ centuries it was already an important food crop, especially for the poor in various countries in Europe. From here, potato spread to all over the world as a major food crop (Harris, 1992).

The genus *Solanum* comprises of many species of which over 200 are tuber bearing according to the latest taxonomic interpretation by Hawkes (1990). Within this genus, the section Tuberarium (Correll, 1962), also known as section Petota (D'Arcy, 1972), includes the tuber-bearing members, of which the cultivated potato is best known. Solanaceous plants can be found throughout the world, though most species dwell in tropical regions of Central and South America.

Potatoes can be grown wherever it is neither too hot (ideally average daily temperatures below 21 $^{o}$C) nor too cold (above 5 $^{o}$C), and there is adequate water from rain or irrigation (Govindakrishan and Haverkort, 2006). The growing season can be as short as 75 days in the lowland subtropics, where 90-120 days is the norm, and as long as 180 days in the high Andes. In the lowland temperate regions where planting is done in spring and harvesting in autumn, crop duration is typically 120-150 days, and yields are potentially high. Average fresh-weight yields vary tremendously by country from 2 to 45 t ha$^{-1}$ with a global average of 17.4 t ha$^{-1}$ (FAOSTAT, 2010). Like many other important crops, potato is a polyploid. Cultivated potato varieties are tetraploid (4n = 48) and many wild species are diploid (2n = 24) but may range up to hexaploid (6n = 72). Besides, potato is outcrossing in nature and phenotypic and genotypic variation is very common in potato. Therefore potato is heterozygous, a characteristic that contributes to its extreme genetic diversity and has probably been a key factor in its survival.

Potato is among the world's most important agronomic crops and is the highest

ranked non-cereal. The role of potato is now well recognised in human nutrition, food security, and national economy of many countries. Due to increasing food demand and changing diets the traditionally high consumption of potatoes in Europe and North America has recently combined with potato becoming a subsistence crop in many other regions particularly in areas where poverty is highly concentrated (Scott, 2002; http://www.cipotato.org). Currently the crop is grown at a significant scale in about 130 countries, and covers yearly worldwide about 18 million ha (Struik and Wiersema, 1999; FAOSTAT, 2010).

Potato high yield potential and high nutritional quality has made them one of the most important plant food sources. It is a wholesome food with all the extremely important and necessary dietary constituents, which are needed for health and growth (Pushkarnath, 1978; Li, 1985; Burton, 1989) (Figure 1.1).

Compared to other roots and tubers and also many cereals, potato tubers have a high ratio protein to carbohydrates with a high nutritional value of the protein (Shekhawat et al., 1994). Potato can be used not only as a human food or animal feed, but also for seed tuber production, and industrial use. Various food processing industries use potato to produce crisps, French fries, flakes, and canned potato, whereas the non-food industry uses potatoes to produce starch, alcohol, etc. (Feustel, 1987; Struik and Wiersema, 1999; Khurana et al., 2003).

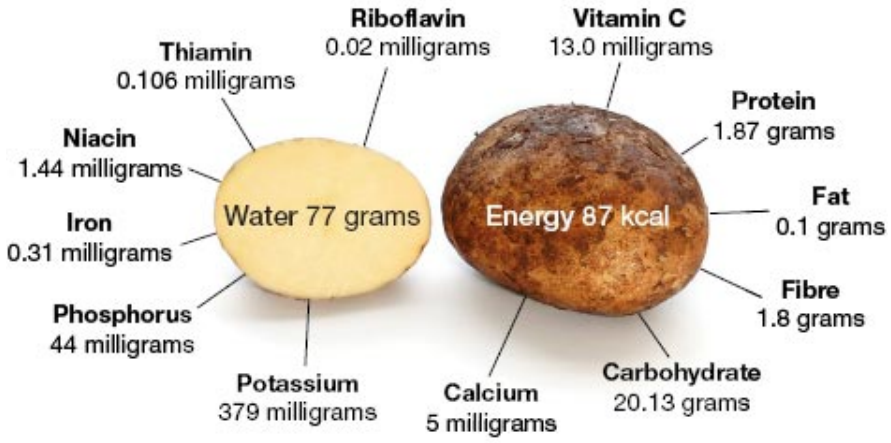


**Figure 1.1.** Nutrient content of potatoes per 100 g, after boiling in skin and peeling before consumption. Source: United States Department of Agriculture, National Nutrient Database.

In short, potato as a major food staple is contributing to the United Nations Millennium Development goals of providing food security and eradicating poverty. In recognition of these important roles, the UN named 2008 as the International Year of

Potato. With the growing global potato production requires modernisation of crop improvement techniques and efficient utilisation of resources towards high yield production.

**Yield determining components in potato**

Yield production can be expressed as the integrated response of distinct plant processes to resources such as radiation, nitrogen or water. This response involves the following two main steps: the production of photoassimilates, and their further transformation into an economic (usually harvestable) component. In potato tuber dry matter yield can be quantified by the summation of the daily incoming photosynthetically active radiation (PAR) times the daily fraction of that radiation intercepted by the crop times the radiation use efficiency times the daily fraction of the total dry matter partitioned to the tubers (Struik et al., 1990). This is illustrated by the following equation:

$$\text{Yield} = \sum\left(\text{PAR}_{\text{inc}} \times f\text{PAR}_{\text{int}}\right) \times \text{RUE} \times \text{HI} \qquad 1.1$$

where $\text{PAR}_{\text{inc}}$ = daily incoming photosynthetically active radiation, $f\text{PAR}_{\text{int}}$ = fraction of the PAR intercepted, RUE = radiation use efficiency, and HI = the harvest index.

The seasonal rate of dry matter accumulation in potato is a function of interception and utilisation of incident photosynthetic active radiation. Differences in the rate of dry matter accumulation can be attributed to differences in light interception caused by variability in maximum LAI (leaf area index), in leaf senescence (e.g., 'canopy cover' in potato) during tuber bulking, and in canopy-level efficiency of utilisation of intercepted radiation as a result of changes in the functionality of leaf photosynthesis during tuber bulking (Pashiardis, 1988; Spitters, 1988; Van Delden et al., 2001). Several authors (Allen and Scott, 1980; Burstall and Harris, 1983; Van der Zaag and Doornbos, 1987; Spitters, 1988; Kooman et al., 1996) have analysed the differences in yield of potato crops based on intercepted radiation, the efficiency of the use of this radiation for dry matter production, and the harvest index.

The genetic improvement of yield can be understood more mechanistically by inspecting and interpreting the relationships between the main attributes of growth and by partitioning the yield components described above. Studies on the mechanistic basis by which breeding has successfully increased yield may shed light on potential future alternatives.

**Need of this study**

The agronomy and physiology of yield development in potato is extremely complex due to genotype specific and environmental effects (i.e. G×E) on crop physiological and morphological characteristics that are conditioned by the combination of genotype and environment, i.e. G×E (Pashiardis, 1988; Allen and Scott, 1992; Jefferies and MacKerron, 1993; Tourneux et al., 2003; Schittenhelm et al., 2006). Despite the importance of this fact, few studies sought to understand the physiological processes leading to yield development and the factors affecting these processes and these are still not well understood. Most reports are concerned with experiments carried out in growth rooms, which often use very short stem sections as planting material and in which environmental conditions, especially light intensity, differed greatly from those normally prevailing during the period of initiation in the field. Insight into the aboveground shoot development, particularly with respect to canopy cover and its relation with whole-plant physiology are still underdeveloped (Almekinders and Struik, 1996).

Traditionally, crop growth simulation models have principally been used to study and predict crop performance in response to environmental conditions and management practices, whereas genotypic impacts on crop performance (especially in the context of plant breeding where large numbers of genotypes are involved) have received little attention. Little efforts have focused on modelling canopy dynamics in relation to genotype with environment interaction (G×E), presumably due to lack of suitable modelling approaches and data sets. There is a need for a model that includes crop reactions to temperature, day length and soil nitrogen availability on the yield dynamics of the crop (Allen and Scott, 1980; Kooman and Rabbinge, 1996). Such a model may also offer breeders the scope to breed for cultivars which make the most effective use of a given environment.

**Main objectives**

The analysis conducted in this thesis is based primarily on data collected from six contrasting field experiments carried out in Wageningen (52° N latitude), the Netherlands, during 2002, 2004 and 2005. The plant material used in this study consisted of 100 F1 diploid (2n = 2x = 24) potato genotypes derived from a cross between two diploid heterozygous potato clones, SH83-92-488 × RH89-039-16 (Rouppe van der Voort et al., 1997; Van Os, 2006) referred to as SH × RH. Besides, five standard cultivars (i.e. Première, Bintje, Seresta, Astarte, and Karnico) were also included in our studies. The thesis has the following objectives:

- To develop an approach to quantify and analyse the dynamics of important

growth and development related processes (i.e. dynamics of green canopy cover and tuber bulking), where these processes are dissected into biologically meaningful and genetically relevant component traits. We want to study the impact of these processes on tuber yield production under diverse environmental conditions;

- To analyse how these processes are influenced quantitatively by genotype (G), environment (E), and G×E interaction;
- To develop a physiology based unambiguous method of assessing maturity type in potato;
- To identify favourable QTL alleles for yield determining physiological component traits of potato for specific environment(s) to complement marker assisted breeding programmes;
- To examine the ability and potential of the ecophysiological crop growth model 'GECROS' in explaining yield differences in potato to help design strategies for potato ideotype breeding for specific genotypes and/or environments;
- To identify important physiological and genotypic traits which could be useful as a selection criterion for improving crop yield in potato.

**Outline of the thesis**

This thesis is composed of six chapters including this introduction (**Chapter 1**). **Chapters 2** to **5** present the main results of the study. **Chapter 2** and **Chapter 3** describe a modelling approach to analyse and quantify the dynamics of canopy cover and tuber bulking, respectively, during the entire crop cycle as a function of thermal time and its variability among potato genotypes and to break the time course and its variation down into biologically meaningful and genetically relevant component traits. We dissect and assess the role of genotype (G), environment (E), and G×E on tuber yield production; discuss the heritability of these traits and their genetic background (i.e. QTLs) on the paternal genomes. Using this approach, the aim is to quantitatively analyse the sources of variation into useful components of canopy cover and tuber bulking dynamics and get insights into the most vital processes that can be used to explore the possibilities of genetically manipulating potato tuber yield. **Chapter 4** discusses how to quantify and assess maturity type unambiguously for a large set of genotypes. It presents an improved approach to re-define the concept of maturity type in terms of important physiological traits thus relating the maturity to crop phenology and physiology. **Chapter 5** examines the performance of the ecophysiological crop growth model 'GECROS' to analyse differences in tuber yield in a set of varieties covering a wide range of maturity types and a diploid (SH × RH) F1

segregating population of potato. Finally, **Chapter 6** discusses the main findings and overall contribution of this thesis. It concludes with new directions and opportunities of linking crop physiology with genetic systems and indicates ways to enhance the power of molecular breeding strategies in potato. Figure 1.2 illustrates the overall framework of this study, while Figure 1.3 further elaborates that plan and provides a schematic outline of this thesis.

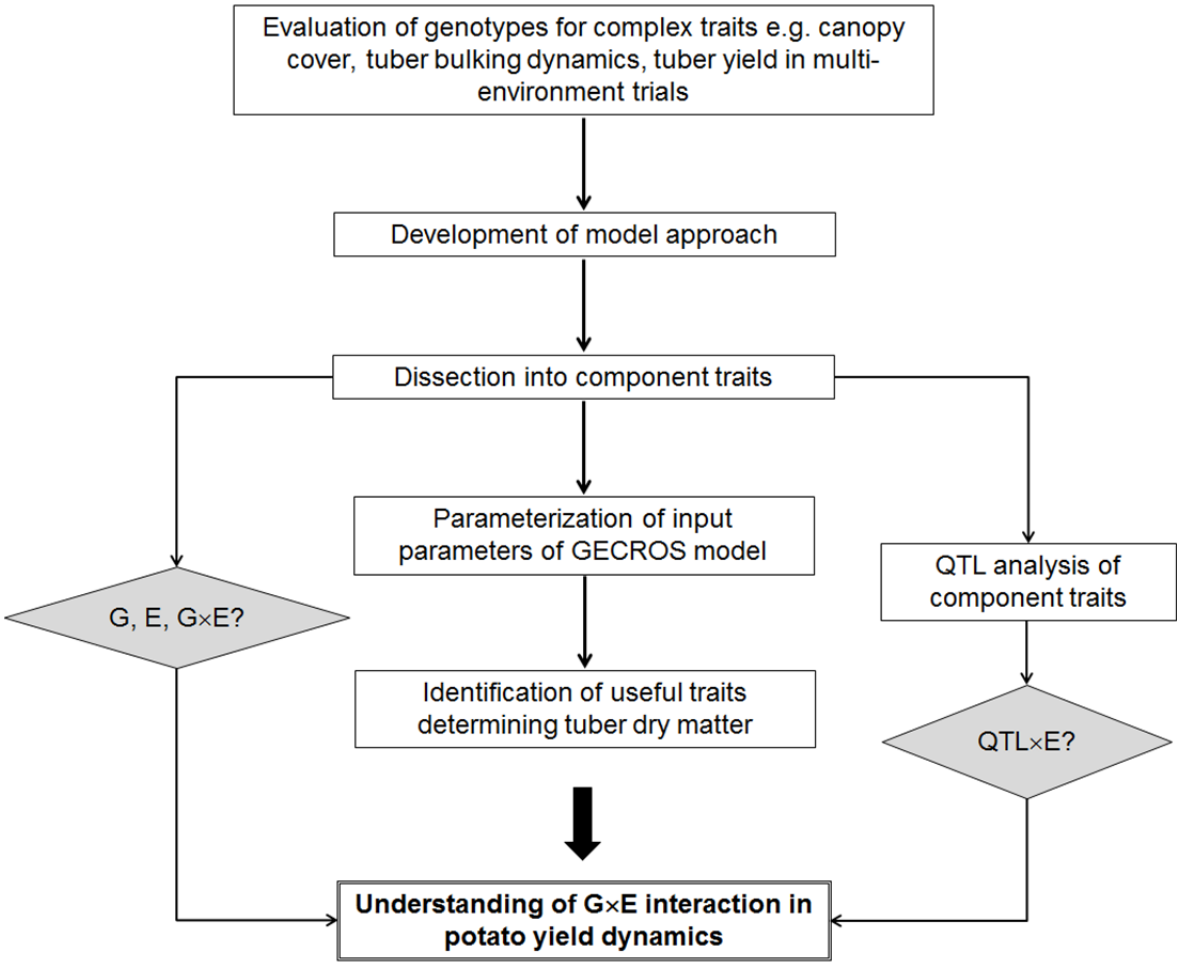


**Figure 1.2.** Overall framework of this study.

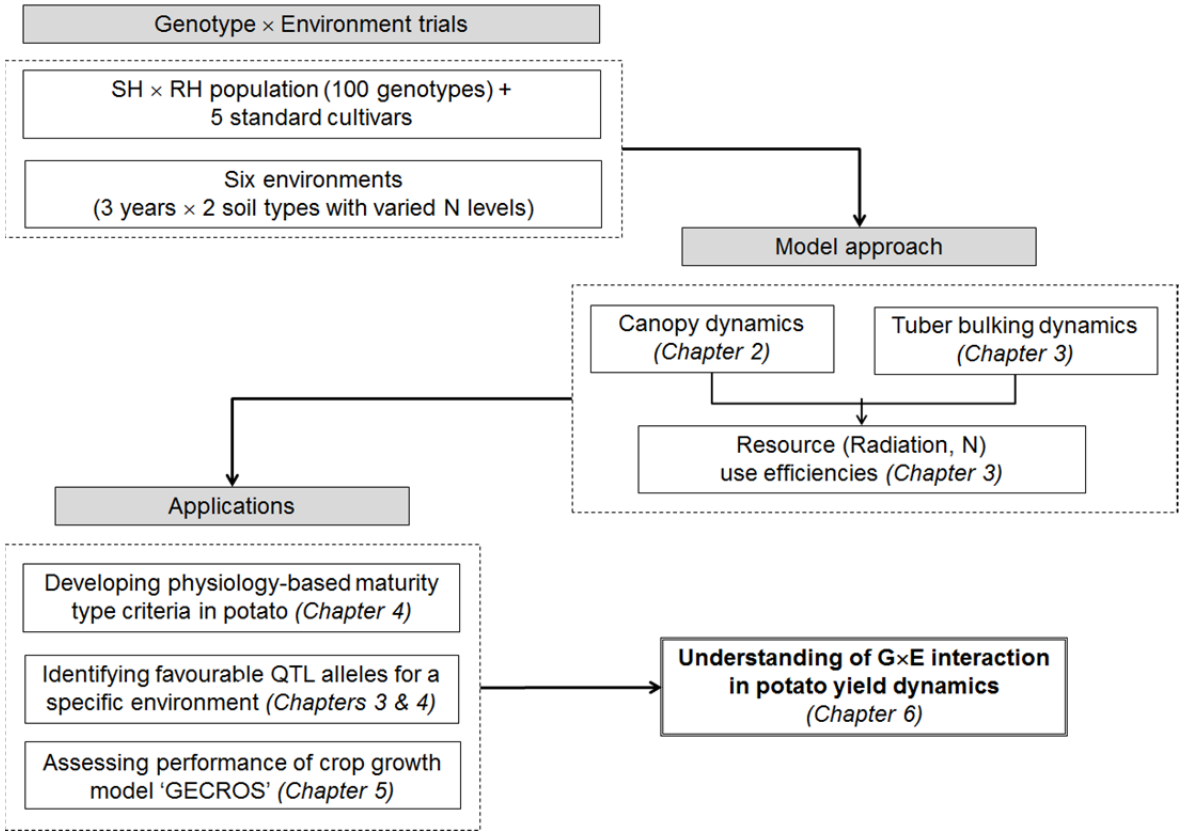


**Figure 1.3.** Schematic thesis outline.

# CHAPTER 2

## Analysing genetic variation in potato (*Solanum tuberosum* L.) using standard cultivars and a segregating population. I. Canopy cover dynamics*

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**Abstract**
We present a model based on the beta function to analyse the genotype-by-environment (G×E) interactions for canopy cover dynamics in potato (*Solanum tuberosum* L.). The model describes the dynamics during the build-up phase, maximum cover phase, and decline phase of canopy development through five parameters defining timing and duration of three phases and maximum canopy cover ($v_{max}$). These five parameters were estimated for 100 individuals of an F1 population, their parents, and five standard cultivars, using data from six field experiments, and used to estimate secondary traits, related to rate of increase or decrease of canopy cover and the area under the canopy cover curve for the three phases. The length of the canopy build-up phase was conserved, but the duration of maximum canopy cover ($D_{P2}$) and the decline phase ($D_{P3}$) varied greatly, with late maturing genotypes having longer $D_{P2}$ and $D_{P3}$ and thus a higher area under whole green canopy cover curve ($A_{sum}$). Genetic variance of the onset ($t_2$) or end ($t_e$) of canopy senescence and $A_{sum}$ contributed greatly to the phenotypic variance. Strong positive phenotypic and genetic correlations were observed between $D_{P2}$ and $v_{max}$ or $t_e$, indicating that genotypes with longer $D_{P2}$ could be indirectly obtained by selecting genotypes with high $v_{max}$ or $t_e$. High broad-sense heritability estimates across six environments were recorded for $t_2$, $t_e$, $D_{P2}$, and $A_{sum}$. Several quantitative trait loci (QTLs) were detected for our model parameters and derived traits explaining the variance by up to 74%; many of these QTLs were located on paternal linkage group V. Some of the QTLs were mapped to similar positions in the majority of environments, but only few QTLs were stable across environments. We conclude that our approach yielded estimates for agronomically relevant crop characteristics for defining future breeding strategies in potato and the information obtained should help in marker- assisted selection.

**Key words:** Potato (*Solanum tuberosum* L.), canopy cover dynamics, beta function, thermal time, components of variance, genotype-by-environment (G×E) interaction, genetic variability, heritability, maturity type, QTL mapping, QTL-by-environment (QTL×E) interaction.

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## 1. Introduction

Tuber dry matter yield in potato (*Solanum tuberosum* L.) can be quantified by the summation of the daily incoming photosynthetically active radiation (PAR) times the daily fraction of that radiation intercepted by the crop times the radiation use efficiency times the daily fraction of the total dry matter partitioned to the tubers (Struik et al., 1990). This paper is on the first part of the equation: the fraction of the incoming radiation intercepted, as in many potato growing regions the ability of the crop to produce and maintain a green canopy able to absorb and use incoming radiation during the available growing season for biomass production determines tuber yields (Moll and Klemke, 1990).

The crop canopy cover at each time during the growing season is the resultant of the rate and duration of canopy growth and the rate of canopy senescence (or the timing of the haulm killing) (Struik et al., 1990; Struik, 2007). This canopy cover directly correlates with the fraction of incoming PAR absorbed (Khurana and McLaren, 1982; MacKerron and Waister, 1985a; Van der Zaag and Doornbos, 1987; Van Delden et al., 2001). Under optimal conditions and with long growing seasons, early establishment of full canopy cover and its persistence over a long period lead to a higher yield due to better interception of incoming radiation (Martin, 1995), although the biomass needs to be partitioned to tubers to obtain economic yield. There is a close, positive correlation between canopy cover and tuber yield (Van der Zaag, 1982; Vander Zaag and Demagante, 1987; Fahem and Haverkort, 1988). The proper quantification of canopy dynamics is therefore one of the most important elements of modelling potato production (Hodges, 1991).

The variation in tuber yield among potato genotypes can – under conditions without abiotic or biotic stress – be analysed in terms of differences in cumulative light absorption, the efficiency with which the absorbed light energy is used for biomass production, and partitioning of dry matter to the desired plant organ (Pashiardis, 1988; Spitters, 1988; Van Delden et al., 2001). Most potato genotypes are indeterminate (Allen and Scott, 1992; Struik and Ewing, 1995, Almekinders and Struik, 1996) and (the continuation of) canopy growth largely depends on the appearance of lateral (basal or sympodial) branches, and on the appearance, expansion, and senescence of leaves on those branches (Allen and Scott, 1992; Vos and Biemond, 1992; Vos, 1995a; Almekinders and Struik, 1996; Fleisher et al., 2006). The canopy cover in potato crops may therefore comprise of leaves from main stems, secondary stems, and axillary branches (Allen, 1978). Potato genotypes differ in the degree to which they branch and the extent of sympodial branching is indicative of their maturity type and the degree of determinacy in their growth habit (Firman et al., 1995). Once tuber bulking has become rapid, the branch formation comes to a halt

and the leaf senescence is no longer compensated by new leaf formation. The duration of canopy cover can be considered a trait reflecting the maturity type of a specific cultivar or genotype (Chapter 4).

Genotypic differences in potato canopy cover are large (Spitters, 1988; Jefferies and MacKerron, 1993; Tourneux et al., 2003). Spitters (1988) for example showed that differences in yields among five contrasting varieties could be explained by variation in canopy cover over time (resulting in differences in cumulative light absorption) and in light use efficiency and harvest index. Like many other complex quantitative traits, canopy cover may be controlled by many interacting genes of which each only has a small effect (Lark et al., 1995; Orf et al., 1999; Daniell and Dhingra, 2002; Stuber et al., 2003). The principal approach for the analysis of quantitative traits is the use of a population which segregates for the traits of interest (Tanksley et al., 1989). For potato, individuals of such a segregating population can be produced by crosses made between commercial cultivars or with individual genotypes developed from population improvement procedures and they are readily propagated by asexual reproduction (Bradshaw, 1994). Commercial cultivars utilised as parents are heterozygous and segregation of characters will be found in the F1 generation following hybridisation.

Canopy cover dynamics also shows a high genotype-by-environment (G×E) interaction (Pashiardis, 1988; Allen and Scott, 1992; Schittenhelm et al., 2006). The main environmental factors influencing the canopy dynamics under field conditions are temperature, photoperiod, light intensity, water supply, and nitrogen (N) supply. For our study the effects of temperature and N are most relevant and these are therefore summarised in this introduction.

Temperature strongly influences stem elongation and branching (Marinus and Bodlaender, 1975; Allen and Scott, 1980; Struik et al., 1989a, Almekinders and Struik, 1994, 1996) and leaf appearance, expansion, and senescence (Kirk and Marshall, 1992; Vos, 1995a; Firman et al., 1995; Struik and Ewing, 1995; Van Delden et al., 2001; Fleisher and Timlin, 2006; Fleischer et al., 2006; Struik, 2007), with optimal and maximum temperatures for these processes contributing to canopy development being 23-25 ˚C and about 32 ˚C, respectively (Struik, 2007). N supply affects the number of lateral (basal and sympodial) branches, the number of leaves on those branches, the individual leaf size and leaf senescence (Fernando, 1958; Humphries and French, 1963; Vos and Biemond, 1992; Almekinders and Struik, 1996). Nitrogen helps to attain complete canopy cover early in the season, especially under relatively resource-poor conditions (Haverkort and Rutavisire, 1986; Vos, 2009), to extend the period of full canopy cover; and to slow down senescence (Santeliz and Ewing, 1981), thus leading to increased light interception (Martin, 1995).

There is a clear need to investigate the components of genetic variation (e.g. in canopy dynamics) and to determine the G×E interaction for a diverse population under contrasting environmental conditions (Tarn et al., 1992; Bradshaw, 1994). The genetic variation and the G×E interaction for canopy cover need to be defined by precisely assessing the rate and duration of the build-up phase, the maximum canopy cover and the duration of the period during which this maximum is maintained and the rate and duration of the canopy senescence. These variables need to be optimised in such a way that the crop can complete its growth cycle within the period of favourable weather conditions thus realising a high yield and an adequate harvest index. There is a growing awareness that in order to better analyse complex traits using increasingly available genomic information, integration of quantitative crop physiology with genetics is required (Tardieu, 2003; Yin et al., 1999a; Yin et al., 2004; Hammer et al., 2006; Yin and Struik, 2008; Chenu et al., 2009; Messina et al., 2009; Hammer et al., 2010; Tardieu and Tuberosa, 2010; Yin and Struik, 2010).

In this paper we first describe a quantitative approach to analyse the time course of canopy cover during the entire crop cycle as a function of thermal time and its variability among potato genotypes and to break the time course and its variation down into biologically meaningful and genetically relevant component traits. Using this approach, we aim to quantitatively analyse the sources of variation in canopy cover dynamics among full-sibs of an outcrossing segregating population, their parents and a set of standard cultivars of potato. The heritability of and genetic variation among different component traits of canopy cover are estimated (Van Eeuwijk et al., 2005). Finally, we perform QTL mapping of our traits to investigate their genetic basis and discuss the co-locations of QTLs for these traits and their QTL-by-environment (QTL×E) interaction. With such information, dominant components of canopy cover can be identified and their phenotypic and genetic correlations can be assessed, with the ultimate goal of designing an effective breeding strategy of potato.

## 2. Materials and methods

### 2.1. *F1 segregating population of SH × RH and standard cultivars*

The plant material used in this study consisted of 100 F1 diploid (2n = 2x = 24) potato genotypes derived from a cross between two diploid heterozygous potato clones, SH83-92-488 × RH89-039-16 (Rouppe van der Voort et al., 1997; Van Os et al., 2006). Parent material was also included in the study. The female parental clone SH82-93-

488 is referred to as "SH" and the male parental clone RH89-039-16 as "RH". Like many other full-sib populations, the SH × RH population segregates for maturity type, which is strongly associated with the duration of canopy cover (Van der Wal et al., 1978; Van Oijen, 1991). It should be noted that diploid potatoes perfectly resemble tetraploid cultivars with respect to many developmental processes, including canopy development, but the most noticeable difference is a somewhat smaller plant size (Hutten, 1994).

We also included five standard (tetraploid) cultivars in our studies: Première, Bintje, Seresta, Astarte and Karnico. These cultivars were chosen because of their differences in maturity type when grown in the Netherlands and they ranged from early (Première) to very late (Karnico). This selection of standard cultivars would allow a benchmarking of consequences of maturity type on the time course of canopy cover.

We aimed at using disease-free, uniform-sized seed tubers of similar physiological quality and therefore produced seed tubers under the same conditions and stored them together at 4 ˚C for approximately 6 months until planting. The graded seed tubers were disinfected chemically to control Rhizoctonia and pre-sprouted before planting.

### 2.2. *Field experiments and measurements*

Six field experiments were carried out in Wageningen, the Netherlands (52˚ N latitude), during 2002, 2004, and 2005, with two experiments in each year, to record canopy cover dynamics for 100 F1 genotypes, 2 parents, and 4 (Exps 5 and 6) or 5 (Exps 1-4) standard cultivars. Karnico was not included in the two experiments in 2005. Experiments differed in environmental conditions because they were carried out in different years, on different soils, and under different N fertiliser regimes, thereby creating six contrasting environments (Table 2.1). Each experiment was conducted using a randomised complete block design with two blocks. The genotypes were randomised within each block, consisting of 106 or 107 plots. Each plot had six rows of 16-18 plants. The seed bed was prepared following standard cultivation practices. Seed tubers were planted in rows spaced 0.75 m apart with 0.27-0.30 m between plants within the same rows. Nitrogen fertiliser was broadcasted at planting in amounts depending on experiment (Table 2.1). Soil phosphorus and potassium levels were kept sufficiently high to sustain normal crop growth. Crops were managed well to ensure that they were free of pests, diseases, and weeds. Irrigation was applied when necessary to avoid drought stress.

**Table 2.1.** Description of the experimental sites and experimental methods applied in Wageningen, the Netherlands.

| Experiment no. | 1 | 2 | 3 | 4 | 5 | 6 |
|---|---|---|---|---|---|---|
| Year | 2002 | 2002 | 2004 | 2004 | 2005 | 2005 |
| Soil type | Clay | Sand | Clay | Sand | Sand | Sand |
| Planting pattern (m × m) | 0.75 × 0.30 | 0.75 × 0.30 | 0.75 × 0.27 | 0.75 × 0.27 | 0.75 × 0.27 | 0.75 × 0.27 |
| Planting date | 25 April | 25 April | 28 April | 28 April | 4 May | 26 April |
| Plant density (plants $m^{-2}$) | 4.4 | 4.4 | 4.9 | 4.9 | 4.9 | 4.9 |
| Net plot size ($m^2$) | 23.0 | 23.0 | 20.7 | 20.7 | 20.7 | 20.7 |
| Soil N at planting (kg $ha^{-1}$) | n.d.[1] | n.d.[2] | 12.5 | 23.0 | 81.0 | 49.5 |
| Fertiliser N (kg $ha^{-1}$) | 143 | 175 | 70 | 200 | 125 | 50 |
| Tuber N uptake (kg $ha^{-1}$) † | – | – | 112.3 | 172.0 | 153.6 | 156.1 |

| Weather conditions during growing season | | | |
|---|---|---|---|
| | 2002 | 2004 | 2005 |
| Air temperature max (°C) | 20.9 | 20.6 | 20.7 |
| Air temperature min (°C) | 11.2 | 10.4 | 9.9 |
| Rainfall (mm) | 364.1 | 367.1 | 369.1 |
| Relative humidity (%) | 78.2 | 75.6 | 76.5 |
| Solar radiation (MJ $m^{-2}$ $d^{-1}$) | 15.3 | 15.8 | 15.8 |

[1] n.d. = no data. Guestimate: 40 kg N $ha^{-1}$.

[2] n.d. = no data. Guestimate: 60 kg N $ha^{-1}$.

† Data for Experiments 1 and 2 were not available and replaced by "–".

Plant emergence date was observed on the date when 50% of the plants had emerged from the soil surface. Afterwards, green canopy cover (%) was visually assessed on weekly basis for each plot during the whole crop cycle by using a grid as

described by Burstall and Harris (1983). The grid consisted of an aluminium frame with the dimensions 0.75 m × 0.90 m, adjusted to the common planting pattern for potato (row width 0.75 m, planting distance within the row 0.30 m). The frame was divided into 100 equal rectangles of 0.075 m × 0.090 m. The grid was placed above the potato canopy at 1 m from the ground and only those rectangles more than half filled with green leaves were counted by observing vertically above to avoid parallax error (Cadersa and Govinden, 1999). The grid was placed half way on each side of the potato row to sample three plant positions. Observations were always made at the same position in the field. The number of observations made on the canopy cover during the growing season per individual plot was 17-21.

At the end of the growing season, tubers of each plot were harvested and dried in an oven at 70 ˚C to constant weight. In samples of the growing seasons of 2004 and 2005, tuber nitrogen content was determined by micro-Kjeldahl digestion and distillation (AOAC, 1984) in a fully accredited commercial laboratory. Average N uptake was calculated and was used to characterise some of the environments in terms of total N available for crop growth.

## 2.3. *Model approach*

### 2.3.1. A model for phasic development of canopy cover dynamics

Canopy cover dynamics in potato as quantified by the grid method typically follows a pattern that can be subdivided into three distinct phases (Fig. 2.1), i.e. build-up phase (*P*1), maximum cover phase (*P*2), and decline phase (*P*3).

#### *Build-up phase (P1)*

This first phase covers the period from emergence to full canopy cover, and is dominated by appearance of stems, lateral branches and leaves, and expansion of those organs (Allen and Scott, 1992; Vos and Biemond, 1992; Vos, 1995a; Fleisher et al., 2006). To obtain flexible and asymmetrical curves, canopy cover during *P*1 can be written, according to a sigmoid part of the beta function for determinate growth (Yin et al., 2003a), as:

$$v = v_{\max}\left(1+\frac{t_1-t}{t_1-t_{\mathrm{m1}}}\right)\left(\frac{t}{t_1}\right)^{\frac{t_1}{t_1-t_{\mathrm{m1}}}} \quad \text{with} \quad 0 \le t \le t_1 \qquad (2.1)$$

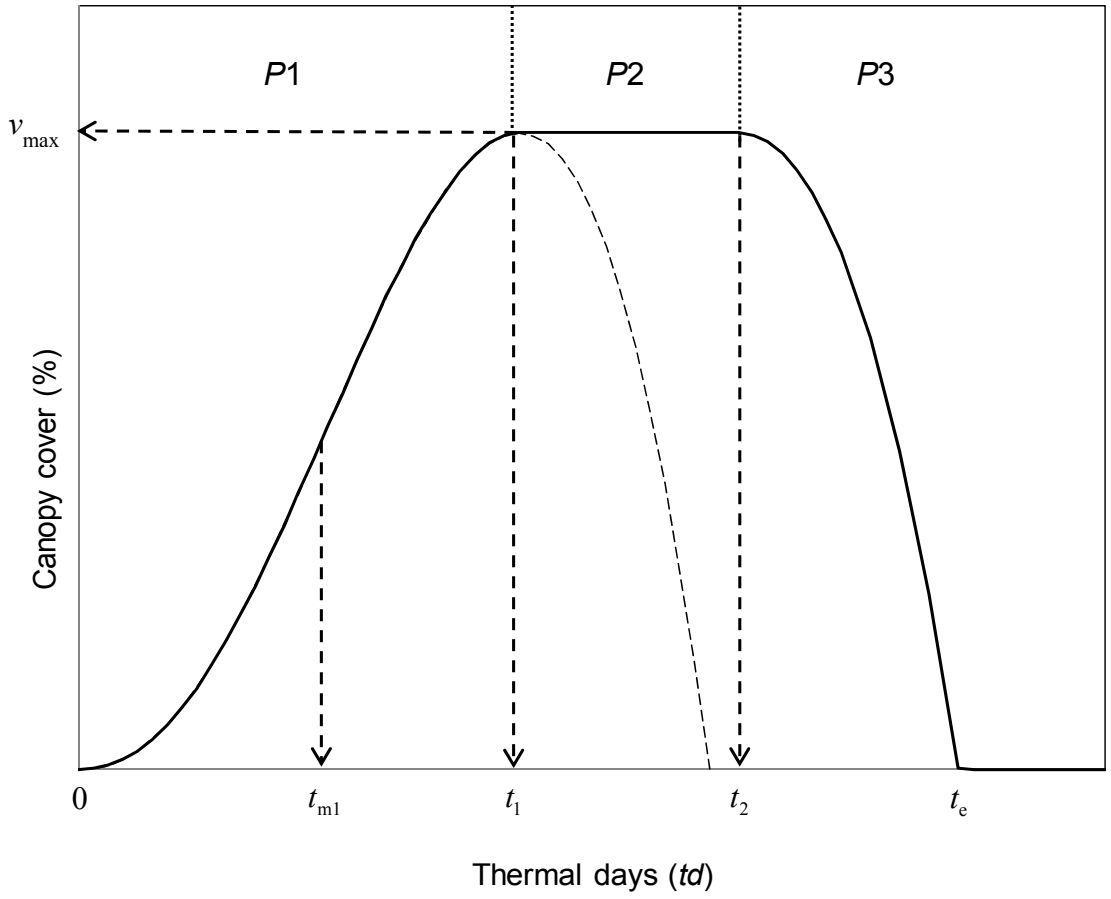


**Figure 2.1.** Temporal course of potato canopy development (full curve) from time 0 to $t_e$ described by our three-phase model, eqns (2.1-2.3), respectively. *P*1 (canopy build-up phase), *P*2 (maximum canopy cover phase), and *P*3 (canopy decline phase). The dashed curve is the mathematical extension of eqn (2.1).

where $t_{m1}$ is the inflexion point and $v_{max}$ is the maximum value of canopy cover $v$, which is reached at time $t_1$ (Fig. 2.1). Equation (2.1) can be applied to canopy cover within the time span of $0 \le t \le t_1$; otherwise, $v$ has to be set at 0 if $t < 0$ or at $v_{max}$ if $t > t_1$.

***Maximum cover phase (P2)***

During this phase the canopy cover retains its maximum level $v_{max}$. The canopy cover during *P*2 is simply given by:

$$v = v_{max} \quad \text{with} \quad t_1 \le t \le t_2 \tag{2.2}$$

where $t_2$ reflects the last time point when canopy cover is still at its maximum and/or onset of canopy senescence (Fig. 2.1).

***Decline phase* (*P3*)**

The canopy cover starts to decline after time $t_2$, and reaches zero at the end of the crop cycle i.e. $t_e$. Usually this decline follows a reversed sigmoid pattern, which could be formulated as $v_{max}[1\text{-}f(t)]$ (cf. Yin et al., 2009), where $f(t)$ is the function, such as eqn (2.1), describing a normal sigmoid pattern with time. Therefore, for *P*3, an equation could be formulated, using an inflexion point of the decline phase. However, in many cases the estimates for parameters showed large standard errors, indicating over-fitting when a model having this inflexion is applied in combination with eqns (2.1) and (2.2) to describe the data of the entire time course of canopy dynamics. To reduce the chance of over-fitting, we developed an equation for the canopy cover in Phase 3 excluding this second inflexion, yet yielding satisfactory results:

$$v = v_{\max}\left(\frac{t_e - t}{t_e - t_2}\right)\left(\frac{t + t_1 - t_2}{t_1}\right)^{\frac{t_1}{t_e - t_2}} \quad \text{with} \quad t_2 \le t \le t_e \qquad (2.3)$$

where $t_e$ reflects the time point when canopy cover is zero. This equation is based on a decline part of the beta equation (Yin et al., 1995) and assumes that $t_e$ differs from the extended end point of eqn (2.1) by ($t_2$-$t_1$) (Fig. 2.1). Equation (2.3) can be applied within the time span of $t_2 \le t \le t_e$; otherwise, $v$ has to be set at 0 if $t > t_e$.

Combining eqns (2.1, 2.2, and 2.3) yields a model with five parameters: $t_{m1}$, $t_1$, $t_2$, $t_e$, and $v_{max}$. Any further reduction of parameters resulted in significant loss of fit (data not shown). The model describes canopy dynamics for a given genotype-environment combination. The model contains three segments but is smooth because the first derivatives of $v$ with respect to $t$ are zero at the joining points $t_1$ and $t_2$. Values of model parameters $t_{m1}$, $t_1$, $t_2$, $t_e$, and $v_{max}$ were estimated for each individual plot of every experiment with the iterative non-linear least-square regression using the Gauss method, as implemented in the PROC NLIN of the SAS software (SAS Institute Inc., 2004).

### 2.3.2. Calculating secondary traits

Once the model parameters were estimated, several secondary traits were derived reflecting the duration of the phases, the rates of canopy cover dynamics, and the overall potential to intercept light during the different phases.

As defined earlier, our model sets time zero as the onset of *P*1; so the duration of *P*1 is numerically equal to $t_1$, and the duration of the entire cycle is numerically equal to $t_e$. The duration of *P*2 ($D_{P2}$) was calculated as $t_2-t_1$. The duration of *P*3 ($D_{P3}$) was calculated as $t_e-t_2$.

Average growth rate for *P*1 ($c_1$) is defined as: $v_{max}/t_1$, and average senescence rate during *P*3 ($c_3$) is $v_{max}/D_{p3}$. Maximum growth rate during *P*1 ($c_{m1}$), which is achieved at $t_{m1}$, could be estimated according to the equation given by (Yin et al., 2003a) as:

$$c_{m1} = \frac{2t_1 - t_{m1}}{t_1(t_1 - t_{m1})}\left(\frac{t_{m1}}{t_1}\right)^{\frac{t_{m1}}{t_1 - t_{m1}}} v_{max} \tag{2.4}$$

The area under each section of the curve was estimated by integrating eqns (2.1, 2.2, and 2.3) over time for the respective phases. In analogy to the solution to the area for a reversed sigmoid curve (Yin et al., 2009), the integral for *P*1 can be expressed as:

$$A_1 = v_{max}\left[\frac{2t_1(t_1 - t_{m1})}{3t_1 - 2t_{m1}}\right] \tag{2.5}$$

The integral for *P*2 is simply expressed as:

$$A_2 = v_{max}(t_2 - t_1) \tag{2.6}$$

The integral for *P*3 is more complicated and can be found as:

$$A_3 = \frac{v_{max}(t_e - t_2)}{2t_e - 2t_2 + t_1}\left[(t_e - t_2 + t_1)\left(\frac{t_e - t_2 + t_1}{t_1}\right)^{\frac{t_1}{t_e - t_2}} - 2t_1\right] \tag{2.7}$$

The sum of $A_1$, $A_2$, and $A_3$ results in the area under whole green canopy curve, $A_{sum}$. The value of $A_{sum}$ reflects the capability of the crop to intercept solar radiation during the whole growing season (cf. Vos 1995b, 2009).

### 2.4. *Calculating thermal time*

Our experiments were conducted under field conditions. To take account of diurnal and seasonal variation in temperature under these conditions, the time axis in the

above equations should be in thermal time, which has long ago been introduced as a scale of reference for ontogeny (Gallagher, 1976, 1979; Milford and Riley, 1980; Ong, 1983, Milford et al., 1985; Bonhomme, 2000).

We followed the approach of Yin et al. (1995, 2005), who developed an equation to describe the non-linear relationship between temperature ($T$) and rate of growth or of development ($g(T)$) as a function of three cardinal temperatures, i.e. base ($T_b$), optimum ($T_o$) and ceiling temperature ($T_c$):

$$g(T) = \left[ \left( \frac{T_c - T}{T_c - T_o} \right) \left( \frac{T - T_b}{T_o - T_b} \right)^{\frac{T_o - T_b}{T_c - T_o}} \right]^{c_t} \qquad (2.8)$$

where $c_t$ is the temperature response curvature coefficient. When $T \leq T_b$ or $\geq T_c$, growth or development does not take place. When temperature is between $T_b$ and $T_c$, $g(T)$ has a bell-shaped curve with maximum value 1 at $T_o$.

We used data sets of leaf appearance and leaf expansion rates from growth chamber experiments of Fleisher et al. (2006) and Fleisher and Timlin (2006) to estimate the values of $T_b$, $T_o$, $T_c$, and $c_t$ of eqn (2.8). Their data on individual leaf area ($cm^2$) and leaf appearance rate (leaves $plant^{-1}$ $day^{-1}$) of potato cultivar Kennebec was used to estimate leaf area per plant ($cm^2$ $plant^{-1}$) at six (14/10, 17/12, 20/15, 23/18, 28/23, and 34/29 ˚C for day/night) temperatures with a 16/8 h diurnal cycle under ambient [$CO_2$] of 370 µmol $mol^{-1}$. From this data set the values of $T_b$, $T_o$, $T_c$, and $c_t$ were determined using the iterative procedure of SAS-NLIN, which follows a non-linear least squares method for estimation of parameters (SAS Institute Inc., 2004). Estimates (± standard errors) were: $T_b$ = 5.5 (±5.2) ˚C, $T_o$ = 23.4 (±0.5) ˚C, $T_c$ = 34.6 (±1.3) ˚C, $c_t$ = 1.6 (±0.5). Based on the dataset, much extrapolation was involved in estimating $T_b$ which resulted in high standard error. Obviously, we have to assume that the temperature responses were the same for all genotypes and for all phases, based on assertions that within a crop species, the genetic differences in temperature sensitivity of phenology are relatively small (Ellis et al., 1990) and that cardinal temperatures in various developmental processes are quite close in potato (e.g. Struik, 2007). A sensitivity analysis showed that uncertainties in cardinal-temperature values had little impact on assessing genetic differences in canopy development (data not shown).

After the estimation of the temperature response parameters, eqn (2.8) was used to convert days after emergence into thermal days after emergence (*td*). Because the function $g(T)$ is non-linear and temperature fluctuates diurnally, $g(T)$

was estimated on an hourly basis and hourly $g(T)$ values were averaged to obtain the daily value (Yin et al., 2005a). By definition, one thermal day is equivalent to one actual day only if temperature at any moment of that day is at $T_o$ (= 23.4 ˚C). Obviously, every actual day was less than one unit thermal day. Required data of hourly air temperatures were obtained from a weather station in Wageningen located nearby the experimental sites.

## 2.5. *Statistical and genetic analyses*

All statistical analyses were performed in Genstat (Payne et al., 2009). A general analysis of variance across environments was performed to test the significance and extent of differences between environments, all genotypes (including the F1 population, the parents, and standard cultivars) and G×E interactions, where the effect of block within environment was included in the model. Means of genotype (G), environment (E), and G×E interaction terms were compared using the Fisher's least significant difference (LSD) test. Further statistical analyses were performed using only the 100 genotypes of the F1 population and these are described below.

### 2.5.1. Estimation of variance components

We used a statistical model (Van Eeuwijk, 2003) to estimate the variance components and to assess what the contribution was of the genotypic main effects and the G×E to the total phenotypic variance for the model parameters (i.e. $t_{m1}$, $t_1$, $t_2$, $t_e$, and $v_{max}$) and secondary traits ($c_{m1}$, $c_1$, $c_3$, $D_{P2}$, $D_{P3}$, $A_1$, $A_2$, $A_3$, and $A_{sum}$):

$$\underline{y}_{ijk} = \mu + \underline{E}_j + \underline{\beta}_{jk} + \underline{G}_i + \underline{GE}_{ij} + \underline{\varepsilon}_{ijk} \qquad (2.9)$$

where $i$ = 1,..., 100; $j$ = 1,..., 6; $k$ = 1, 2; and $\underline{y}_{ijk}$ denotes the response variable of genotype $i$, in environment $j$, block $k$; $\mu$ is the grand mean; $\underline{E}_j$ is the environmental main effect; $\underline{\beta}_{jk}$ stands for block within environment effect; $\underline{G}_i$ is the genetic effect of genotype $i$; $\underline{GE}_{ij}$ is the genotype-by-environment interaction effect for genotype $i$ in environment $j$, and $\underline{\varepsilon}_{ijk}$ is a residual term. The underlined terms were considered as random effects, which were assumed to be normally and independently distributed with zero mean and a proper variance.

The restricted maximum likelihood (REML) procedure was used to estimate the variance components. The significance of the variance components was tested using the likelihood ratio (LR) test (Morrell, 1998). This test determines the contribution of a single (random) factor by comparing the fit (measured as the deviance, i.e. -2 times

the log likelihood ratio) for models with and without the factor. The phenotypic variance, $\sigma^2_{Ph}$ was estimated from these variance component estimates as (Bradshaw, 1994; Falconer and Mackay, 1996; Lynch and Walsh, 1998):

$$\sigma^2_{Ph} = \sigma^2_E + \sigma^2_\beta + \sigma^2_G + \sigma^2_{GE} + \sigma^2_\varepsilon \quad (2.10)$$

where $\sigma^2_E$ = environmental variance, $\sigma^2_B$ = block variance, $\sigma^2_G$ = genetic variance, $\sigma^2_{GE}$ = G×E variance, and $\sigma^2_\varepsilon$ = experimental error variance.

### 2.5.2. Phenotypic and genetic coefficient of variation

Scaling of the variance by the trait mean, i.e. calculating the coefficient of variation provides a more appropriate way to compare traits (Johnson et al., 1955; Houle, 1992). We therefore calculated the coefficient of variation (%) for each model parameter and derived trait across six experiments, according to:

$$CV_X = \frac{\sqrt{\sigma^2_X}}{\mu} \times 100 \quad (2.11)$$

where $\mu$ is the grand mean of the population, and $\sigma^2_X$ is a variance component (i.e. $\sigma^2_{ph}$ or $\sigma^2_G$ or $\sigma^2_E$ or $\sigma^2_{GE}$) from eqn (2.9).

### 2.5.3. GGE biplot analysis

Studying quantitative traits is complicated due to G×E interactions (Uptmoor et al., 2008). GGE biplot analysis is an effective method to fully explore multi-environment trials for G and G×E components of variation. It allows visual examination of the relationships among the test environments, genotypes and the G×E (Yan et al., 2000). For any particular environment, genotypes can be compared by projecting a perpendicular from the genotype symbols to the environment vector, i.e. genotypes that are further along in the positive direction of the environment vector are better performing and vice versa. The greater the distance from the origin to the intersection of a genotype projection on an environment vector, the more this genotype deviates from the average in this environment (Kroonenberg, 1997; Chapman et al., 1997). GGE biplot analysis was performed to analyse the inter-relations among genotypes and environments. GGE biplots were constructed by plotting the first principal component (PC1) scores of the genotypes and the environments against their respective scores for the second principal component

(PC2). The environment-standardised method of Yan (2002) was used.

### 2.5.4. Phenotypic and genetic correlation

Product-moment (Pearson) correlations were calculated, using genotypic means across blocks within trials, among model parameters and secondary traits.

The genetic correlations were estimated using the following equation (Holland, 2006):

$$r_{\mathrm{G}ij} = \frac{\sigma^2_{\mathrm{G}ij}}{\sqrt{\sigma^2_{\mathrm{G}i}\sigma^2_{\mathrm{G}j}}} \qquad (2.12)$$

where $\sigma^2_{\mathrm{G}ij}$ is the estimated genetic covariance between traits *i* and *j*; $\sigma^2_{\mathrm{G}i}$ and $\sigma^2_{\mathrm{G}j}$ are the genetic variances of traits *i* and *j*, respectively. The multivariate REML procedure was used to estimate the genetic variance and covariance estimates (Meyer, 1985; Holland, 2006). The significance of genetic correlations was determined using a *t*-test after a *z*-transformation of the correlation coefficients (Sokal and Rohlf, 1995; Gutteling et al., 2007).

### 2.5.5. Heritability

We estimated the broad-sense heritability ($H^2$) (%) across all six environments by using the estimated variance components of the linear model described as per eqn (2.9), through the following equation (Bradshaw, 1994; Falconer and Mackay, 1996):

$$H^2 = \frac{\sigma^2_{\mathrm{G}}}{\sigma^2_{\mathrm{G}} + \frac{\sigma^2_{\mathrm{GE}}}{n_{\mathrm{e}}} + \frac{\sigma^2_{\varepsilon}}{n_{\mathrm{t}}}} \times 100 \qquad (2.13)$$

where $n_{\mathrm{e}} = 6$ represents the number of environments, and $n_{\mathrm{t}} = 12$ is the product of number of blocks and environments.

The broad-sense heritability ($H^2$) was also estimated for each individual experiment by using the following formula (Bradshaw, 1994):

$$H^2 = \frac{\sigma^2_{\mathrm{G}}}{\sigma^2_{\mathrm{G}} + \frac{\sigma^2_{\varepsilon}}{n_{\mathrm{b}}}} \times 100 \qquad (2.14)$$

where $\sigma^2_G$ = genetic variance; $\sigma^2_\varepsilon$ = experimental error variance, and $n_b$ = 2 represents the number of blocks per individual environment. The variance components were estimated per individual trial basis.

### 2.5.6. Extension of an AFLP marker map of the SH × RH population

The AFLP primer combinations used in this study have been previously applied to create the ultra-dense genetic map of 130 SH × RH genotypes as described in Van Os et al. (2006). As our 100 F1 lines were only partly genotyped for creating that map, 120 new SH × RH genotypes were fingerprinted with AFLP™ (Vos et al., 1995) to make a map for 250 individuals. Genomic DNA was extracted from frozen leaf tissue according to Van der Beek et al. (1992). AFLP markers were generated according to standard protocols with radioactive labels, using four $E_{co}$-$M_{se}$ primer combinations (Vos et al., 1995). The AFLP profiles of the parental clones were compared with an ultra-dense genetic map and AFLP products of equal electrophoretic mobility which segregated in both sets of the lines were identified. The AFLP (only 1:1 segregating markers) were first mapped in the SH × RH mapping population using JoinMap 4.1 (Van Ooijen, 2006) using a bin mapping approach (Van Os et al., 2006). The marker data were split into two sets on the basis of their segregation type. Markers that were heterozygous in the maternal parent (SH) and absent in the paternal parent (RH) were scored as <ab × aa>; "paternal" markers heterozygous in RH and absent in SH were scored as <aa × ab>.

For map construction, recombination frequencies were converted into map units (cM) by the use of the Kosambi function. Only markers with recombination value of ≤ 0.25 were considered as described by Van Os et al. (2006). The maternal and paternal data sets were divided into 12 and 13 linkage groups, respectively. A graphic representation of a map was made by the Map Chart software (Voorrips, 2002).

### 2.5.7. QTL detection

Genstat version 14 (Payne et al., 2009) software was used to identify QTLs for all component traits. Eighty-eight genotypes of our 100 F1 lines were covered in the sample of the aforementioned 250 lines of SH × RH population for the extended marker map; data of these 88 lines were therefore used for detection of QTLs for five model parameters and nine secondary traits. QTL analysis was performed individually for all six experiments (environments).

QTL models were fitted for the two parents separately. Initially, the

conventional Simple Interval Mapping (SIM) procedure as described by Lander and Bostein (1989) and Hackett et al. (2001) was used to scan the genome for the major QTLs per individual environment. A QTL was declared to be significant ($P$<0.05) for the threshold value ($-\log_{10}(P) > 3.4$). Secondly, a more sophisticated QTL mapping procedure, the Composite Interval Mapping (CIM) was performed to increase the reliability of the QTL analysis (Zeng, 1994; Jansen, 1993; Jansen and Stam, 1994; Jansen, 1995). In this method, background markers were selected to take over the role of the putative QTLs as cofactors to reduce the residual variance. In our analysis, background markers closest to the indicated region of putative QTLs with $-\log_{10}(P)$ scores exceeding the threshold were gradually used as cofactors. This procedure was repeated until no further QTLs were found. The percentage of the total phenotypic variation explained by QTLs identified for each trait was estimated as the $R^2$-value.

## 3. Results and discussion

### 3.1. *Model performance in describing canopy cover dynamics of genotypes*

The use of data in thermal days resulted in a more stable parameter estimation than the use of data in days (data not shown), as the confounding effects of diurnal and seasonal temperature fluctuations during the experimental period could effectively be removed using thermal days. The model for the canopy cover dynamics (i.e. combined eqns (2.1, 2.2, and 2.3)) fitted well for each genotype of potato segregating population, their parents and standard cultivars in the entire data set, with $R^2$ values ranging from 0.94 to 1.00 (n = 17-21; data not shown). Figure 2.2 shows the curve-fitting results for the SH and RH parents and for the standard cultivars that were present in each experiment. In most cases, the standard error (SE) values for observed points (i.e. average of two blocks) were much higher during the canopy decline phase than during the first two phases, consistent with the fact that the estimation of $t_e$ involved much extrapolation due to lack of data points in the third phase of canopy growth. Overall, combined eqns (2.1-2.3) could be very useful in analysing the canopy cover dynamics of a diverse set of potato genotypes under various environments and making inferences about the underlying process controlling canopy growth.

### 3.2. *Model parameters and secondary traits*

Usually, the estimated value of each model parameter differed very little between the

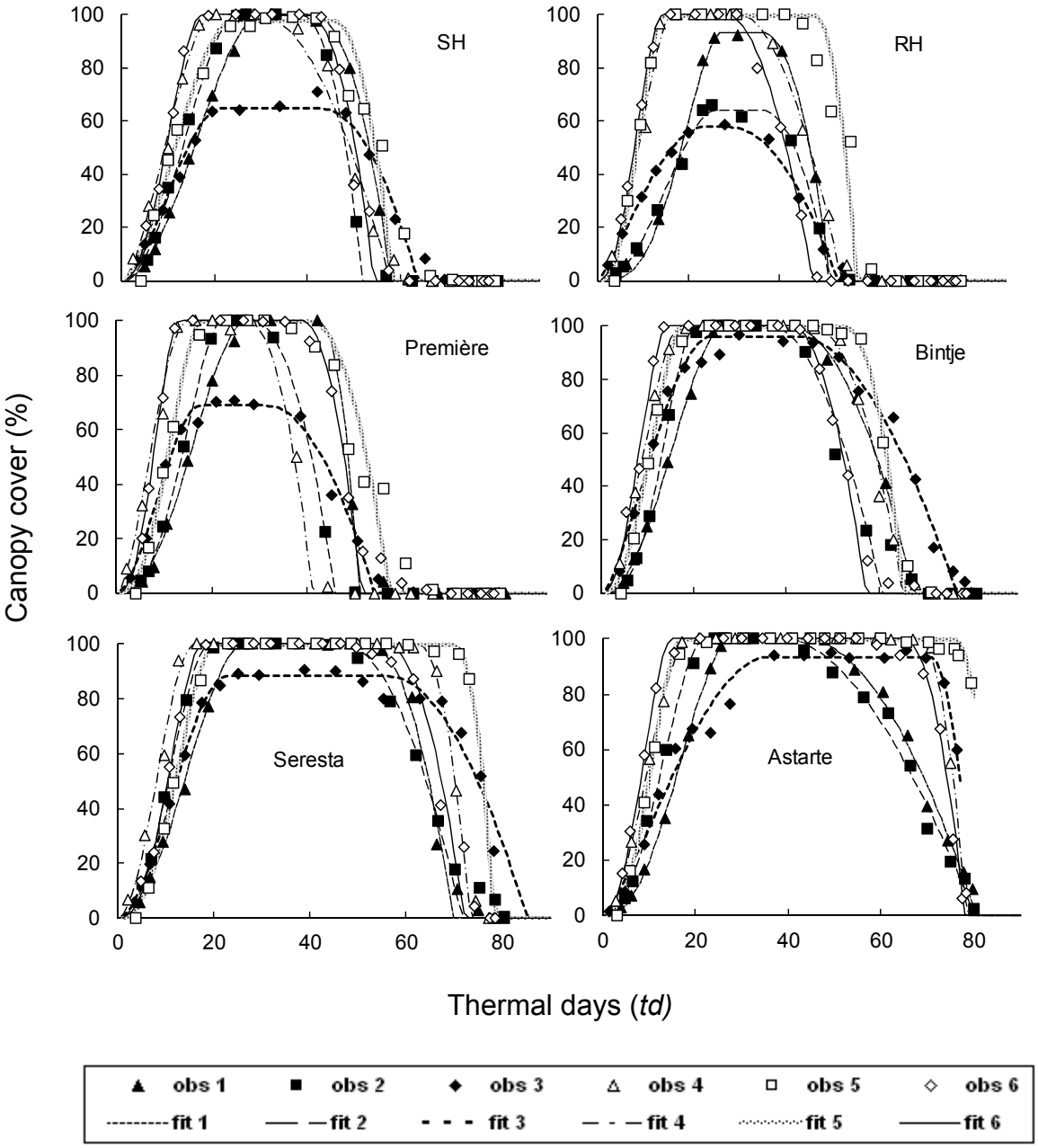


**Figure 2.2.** Observed (obs) points and fitted (fit) curves of standard cultivars and SH and RH parents for all six experiments (environments). Data for cv. Karnico were not available in Exps 5 and 6 (see the text).

two blocks and there was a good positive linear correlation between the two blocks for all model parameters ($R^2$ values usually above 0.7; n = 107). Table 2.2 gives the estimated values of the five model parameters and the nine derived secondary traits for two parents (SH and RH), five standard cultivars, and the mean value of the F1

population for all six environments.

Environment had a highly significant ($P$<0.01) impact on all model parameters and derived secondary traits, at least partly due to the purposeful variation in availability of N across trials (Table 2.1). Nitrogen has a main influence on canopy development (Perumal and Sahota, 1986; Vos, 1995a,b, 2009), arising from effects of N on rate and duration of appearance of leaves and branches on the potato plant, and on the active life span of individual leaves. Due to the lack of precise information about amount of mineral N becoming available during the course of canopy growth, we used the amount of N uptake by tubers as an indicator of N availability (Table 2.1). Crop N uptake is a site-specific indicator of N that is "available" to the crop (Sullivan et al., 2008). Experiments with lower N uptake (especially Exp 3) also had lower estimates for $v_{max}$, $D_{P2}$, and canopy growth rates ($c_{m1}$, $c_1$, and $c_3$). In potato, the duration of $P2$ and whether or not full canopy cover is attained are very much affected by N supply. The total growth period is prolonged for larger rate of N supply because $P2$ extends with better N nutrition. Usually, within agronomically relevant ranges, N has comparatively little effect on $P1$ and affects the rate of senescence only marginally (Vos, 2009). However, in our most extreme experiment (Exp 3) we did observe such effects even to such an extent that the end of the crop cycle (i.e. $t_e$) occurred later in the low N environment (i.e. Exp 3) in comparison to environments with higher N availability (high tuber N uptake) (Table 2.2).

The mean performance of standard cultivars, parental genotypes (SH and RH) and the F1 population across the experimental sites (i.e. environments) varied significantly ($P$<0.01) for all model parameters and secondary traits (Table 2.2). Potato genotypes varied in the duration of the entire crop cycle which is reflected in variation in $t_e$. There were significant differences ($P$<0.05) among the standard cultivars and parents SH and RH for $t_1$, $t_2$, and $t_e$, whereas $t_{m1}$ did not differ significantly among genotypes (Table 2.2). Late cultivars gave higher values for $t_2$ and $t_e$ followed by mid-late and early cultivars. There were small differences among the cultivars for $v_{max}$, but under certain environmental conditions late cultivars might reach higher values than earlier ones, due to their comparatively later tuber set. Kooman and Rabbinge (1996) found that, compared with late cultivars, early potato cultivars allocate a larger part of the available assimilates to the tubers early in the growing season, resulting in shorter growing periods and also lower yields. The initial phase of canopy growth (i.e. $t_1$ or $D_{P1}$) was not much affected by the maturity type of the genotypes, but there were very large differences among standard cultivars for the duration of $P2$ and $P3$ (i.e. $D_{P2}$ and $D_{P3}$, respectively). The duration of $P2$ ($D_{P2}$) tended to be longer for later cultivars. Estimated values of canopy growth rates $c_{m1}$ and $c_1$ varied significantly ($P$<0.05) among the standard cultivars and two parents. However,

**Table 2.2.** Estimated mean values of five model parameters ($t_{m1}$, $t_1$, $t_2$, $t_e$, $v_{max}$) and nine derived secondary traits ($c_{m1}$, $c_1$, $c_3$, $D_{P2}$, $D_{P3}$, $A_1$, $A_2$, $A_3$, $A_{sum}$) as obtained from across environment ANOVA for the two parents (SH and RH) and five standard cultivars (listed in order of increasingly longer crop cycle). *td* stands for thermal day. Data for cv. Karnico were not available in Exps 5 and 6 and are replaced by "–".

| Parameter | Exp. 1 | Exp. 2 | Exp. 3 | Exp. 4 | Exp. 5 | Exp. 6 | Mean¶ |
|---|---|---|---|---|---|---|---|
| $t_{m1}$ (*td*) | | | | | | | |
| SH | 16.0 | 13.5 | 9.4 | 8.8 | 10.8 | 10.2 | 11.4 a |
| RH | 19.7 | 15.3 | 6.2 | 9.6 | 9.4 | 8.7 | 11.5 a |
| Première | 16.3 | 14.8 | 8.4 | 6.7 | 11.7 | 8.4 | 11.1 a |
| Bintje | 15.3 | 14.0 | 8.5 | 8.9 | 11.0 | 8.3 | 11.0 a |
| Seresta | 14.4 | 11.2 | 11.1 | 8.1 | 13.0 | 11.2 | 11.5 a |
| Astarte | 16.8 | 13.0 | 10.0 | 9.3 | 10.9 | 8.6 | 11.4 a |
| Karnico | 14.0 | 12.4 | 9.3 | 8.6 | – | – | 11.1 a |
| Mean† | 16.1 a | 13.5 b | 9.0 d | 8.6 e | 11.1 c | 9.2 d | |
| F1 mean‡ | 18.0 a | 14.7 b | 9.7 e | 10.7 d | 11.6 c | 9.8 e | |
| | | | | | | | |
| $t_1$ (*td*) | | | | | | | |
| SH | 30.1 | 25.0 | 21.5 | 19.9 | 24.1 | 17.4 | 23.0 a |
| RH | 27.6 | 26.1 | 23.6 | 16.5 | 14.7 | 14.4 | 20.5 ab |
| Première | 27.2 | 22.3 | 17.6 | 14.9 | 18.0 | 13.3 | 18.9 b |
| Bintje | 26.8 | 20.2 | 23.8 | 17.2 | 17.8 | 14.4 | 20.0 ab |
| Seresta | 26.3 | 19.1 | 22.6 | 15.9 | 20.1 | 17.7 | 20.3 ab |
| Astarte | 27.9 | 22.1 | 36.0 | 18.6 | 17.0 | 15.1 | 22.8 a |
| Karnico | 23.6 | 19.2 | 31.2 | 16.9 | – | – | 22.7 a |
| Mean† | 27.1 a | 22.0 c | 25.2 b | 17.1 e | 18.6 d | 15.4 f | |
| F1 mean‡ | 31.0 a | 23.0 d | 25.8 b | 19.7 e | 23.8 c | 16.4 f | |

**Table 2.2.** (Continued)

| Parameter | Exp. 1 | Exp. 2 | Exp. 3 | Exp. 4 | Exp. 5 | Exp. 6 | Mean¶ |
|---|---|---|---|---|---|---|---|
| $t_2$ ($td$) | | | | | | | |
| SH | 41.4 | 38.6 | 43.1 | 29.7 | 45.3 | 40.3 | 39.7 cd |
| RH | 36.1 | 35.9 | 29.0 | 31.1 | 47.6 | 28.3 | 34.7 d |
| Première | 42.2 | 28.6 | 31.6 | 28.2 | 40.6 | 38.9 | 35.0 d |
| Bintje | 40.5 | 36.5 | 42.2 | 45.9 | 52.5 | 41.1 | 43.1 c |
| Seresta | 52.1 | 47.0 | 56.3 | 62.4 | 69.8 | 55.7 | 57.2 ab |
| Astarte | 43.2 | 38.8 | 70.3 | 68.0 | 75.7 | 64.9 | 60.2 a |
| Karnico | 31.7 | 28.5 | 75.0 | 72.3 | – | – | 51.9 b |
| Mean† | 41.0 e | 36.2 f | 49.6 b | 48.2 c | 55.3 a | 44.9 d | |
| F1 mean‡ | 41.8 b | 34.0 e | 37.9 d | 40.2 c | 49.0 a | 40.9 bc | |
| | | | | | | | |
| $t_e$ ($td$) | | | | | | | |
| SH | 57.8 | 51.8 | 63.7 | 57.8 | 58.2 | 54.4 | 57.3 e |
| RH | 51.3 | 51.1 | 52.9 | 53.8 | 57.1 | 47.4 | 52.3 f |
| Première | 50.8 | 45.7 | 54.0 | 41.3 | 57.3 | 51.3 | 50.1 f |
| Bintje | 67.7 | 60.6 | 76.9 | 65.3 | 65.5 | 57.2 | 65.5 d |
| Seresta | 69.7 | 71.7 | 85.2 | 73.3 | 78.3 | 72.1 | 75.0 c |
| Astarte | 80.6 | 80.2 | 79.4 | 78.3 | 84.5 | 78.0 | 80.2 b |
| Karnico | 82.9 | 82.5 | 87.5 | 90.4 | – | – | 85.8 a |
| Mean† | 65.8 c | 63.4 d | 71.4 a | 65.7 c | 66.8 b | 60.1 e | |
| F1 mean‡ | 58.2 c | 53.4 e | 62.1 b | 58.1 c | 64.9 a | 57.2 d | |
| | | | | | | | |
| $v_{max}$ (%) | | | | | | | |
| SH | 100.0 | 100.0 | 64.7 | 100.0 | 98.0 | 100.0 | 93.8 c |
| RH | 93.6 | 64.2 | 57.8 | 100.0 | 100.0 | 100.0 | 85.9 d |
| Première | 100.0 | 100.0 | 68.9 | 99.8 | 100.0 | 100.0 | 94.8 bc |
| Bintje | 100.0 | 100.0 | 96.1 | 100.0 | 100.0 | 100.0 | 99.4 ab |
| Seresta | 100.0 | 99.9 | 88.2 | 100.0 | 100.0 | 100.0 | 98.0 abc |
| Astarte | 100.0 | 100.0 | 93.6 | 100.0 | 100.0 | 100.0 | 98.9 ab |
| Karnico | 100.0 | 100.0 | 100.0 | 100.0 | – | – | 100.0 a |
| Mean† | 99.1 b | 94.9 c | 81.3 d | 100.0 a | 99.7 ab | 100.0 a | |
| F1 mean‡ | 95.3 d | 99.2 ab | 71.0 e | 98.8 b | 97.5 c | 99.9 a | |

**Table 2.2.** (Continued)

| Parameter | Exp. 1 | Exp. 2 | Exp. 3 | Exp. 4 | Exp. 5 | Exp. 6 | Mean¶ |
|---|---|---|---|---|---|---|---|
| $c_{m1}$ (% $d^{-1}$) | | | | | | | |
| SH | 5.1 | 6.4 | 4.7 | 7.4 | 6.0 | 9.5 | 6.5 b |
| RH | 6.6 | 4.1 | 3.6 | 9.6 | 11.7 | 11.7 | 7.9 a |
| Première | 6.0 | 7.9 | 5.9 | 9.9 | 9.7 | 13.0 | 8.8 a |
| Bintje | 6.0 | 9.3 | 5.9 | 9.0 | 10.3 | 11.2 | 8.6 a |
| Seresta | 5.9 | 8.5 | 6.0 | 9.5 | 9.3 | 9.7 | 8.2 a |
| Astarte | 5.9 | 7.6 | 3.9 | 8.4 | 10.1 | 10.8 | 7.8 ab |
| Karnico | 7.0 | 9.0 | 4.8 | 8.9 | – | – | 7.4 ab |
| Mean† | 6.1 e | 7.5 d | 5.0 f | 9.0 c | 9.5 b | 11.0 a | |
| F1 mean‡ | 5.1 e | 7.6 c | 4.3 f | 8.7 b | 7.0 d | 10.4 a | |
| | | | | | | | |
| $c_1$ (% $td^{-1}$) | | | | | | | |
| SH | 3.3 | 4.1 | 3.0 | 5.0 | 4.1 | 5.9 | 4.2 b |
| RH | 3.4 | 2.5 | 2.5 | 6.0 | 6.8 | 7.0 | 4.7 b |
| Première | 3.7 | 4.5 | 3.9 | 6.7 | 5.6 | 7.5 | 5.3 a |
| Bintje | 3.7 | 5.0 | 4.0 | 5.9 | 5.7 | 7.0 | 5.2 ab |
| Seresta | 3.8 | 5.3 | 3.9 | 6.3 | 5.1 | 5.7 | 5.0 ab |
| Astarte | 3.6 | 4.6 | 2.7 | 5.4 | 5.9 | 6.7 | 4.8 ab |
| Karnico | 4.3 | 5.2 | 3.2 | 5.9 | – | – | 4.7 b |
| Mean† | 3.7 e | 4.4 d | 3.3 f | 5.9 b | 5.5 c | 6.6 a | |
| F1 mean‡ | 3.1 d | 4.4 c | 2.8 e | 5.2 b | 4.4 c | 6.2 a | |
| | | | | | | | |
| $c_3$ (% $td^{-1}$) | | | | | | | |
| SH | 6.1 | 7.6 | 3.2 | 3.9 | 8.1 | 8.2 | 6.2 a |
| RH | 6.2 | 4.3 | 2.5 | 4.6 | 11.1 | 5.2 | 5.7 a |
| Première | 11.6 | 5.9 | 3.1 | 7.4 | 6.7 | 8.1 | 7.1 a |
| Bintje | 3.8 | 5.0 | 2.8 | 5.4 | 8.6 | 6.3 | 5.3 a |
| Seresta | 5.7 | 4.1 | 7.3 | 11.2 | 11.9 | 7.2 | 7.9 a |
| Astarte | 2.7 | 2.5 | 11.0 | 9.7 | 12.7 | 8.5 | 7.9 a |
| Karnico | 2.0 | 1.9 | 8.1 | 8.0 | – | – | 5.0 a |
| Mean† | 5.4 c | 4.5 d | 5.4 c | 7.2 b | 9.9 a | 7.2 b | |
| F1 mean‡ | 6.5 b | 6.1 b | 3.4 c | 6.4 b | 7.5 a | 7.1 a | |

**Table 2.2.** (Continued)

| Parameter | Exp. 1 | Exp. 2 | Exp. 3 | Exp. 4 | Exp. 5 | Exp. 6 | Mean¶ |
|---|---|---|---|---|---|---|---|
| $D_{P2}$ (*td*) | | | | | | | |
| SH | 11.3 | 13.6 | 21.5 | 9.8 | 21.3 | 22.9 | 16.7 c |
| RH | 8.5 | 9.8 | 5.3 | 14.5 | 33.0 | 13.8 | 14.2 c |
| Première | 15.0 | 6.2 | 14.1 | 13.3 | 22.7 | 25.6 | 16.1 c |
| Bintje | 13.7 | 16.3 | 18.4 | 28.7 | 34.7 | 26.7 | 23.1 b |
| Seresta | 25.8 | 27.9 | 33.6 | 46.5 | 49.7 | 38.1 | 36.9 a |
| Astarte | 15.4 | 16.7 | 34.3 | 49.4 | 58.8 | 49.8 | 37.4 a |
| Karnico | 8.1 | 9.3 | 43.8 | 55.4 | – | – | 29.1 b |
| Mean† | 14.0 e | 14.2 e | 24.4 d | 31.1 b | 36.7 a | 29.5 c | |
| F1 mean‡ | 10.7 d | 11.1 cd | 12.0 c | 20.5 b | 25.1 a | 24.5 a | |
| | | | | | | | |
| $D_{P3}$ (*td*) | | | | | | | |
| SH | 16.5 | 13.2 | 20.7 | 28.1 | 12.9 | 14.1 | 17.6 bc |
| RH | 15.1 | 15.3 | 23.9 | 22.7 | 9.5 | 19.2 | 17.6 bc |
| Première | 8.7 | 17.2 | 22.4 | 13.1 | 16.7 | 12.4 | 15.1 c |
| Bintje | 27.1 | 24.2 | 34.7 | 19.4 | 13.0 | 16.1 | 22.4 b |
| Seresta | 17.6 | 24.7 | 28.9 | 10.9 | 8.5 | 16.4 | 17.8 bc |
| Astarte | 37.4 | 41.5 | 9.1 | 10.3 | 8.8 | 13.1 | 20.0 bc |
| Karnico | 51.3 | 54.0 | 12.5 | 18.1 | – | – | 34.0 a |
| Mean† | 24.8 b | 27.1 a | 21.7 c | 17.5 d | 11.6 f | 15.2 e | |
| F1 mean‡ | 16.5 d | 19.4 b | 24.3 a | 17.9 c | 16.0 d | 16.3 d | |
| | | | | | | | |
| $A_1$ (*td %*) | | | | | | | |
| SH | 1455.5 | 1192.3 | 723 | 1047.7 | 1239.1 | 785.4 | 1074 a |
| RH | 946.2 | 743.1 | 810 | 753.8 | 610 | 636 | 750 b |
| Première | 1201.1 | 900.3 | 612.3 | 777 | 738.7 | 561.2 | 798 b |
| Bintje | 1231.3 | 763.7 | 1286.5 | 844.4 | 756.8 | 658.7 | 924 ab |
| Seresta | 1247.5 | 862 | 1011.7 | 786.5 | 827.7 | 745.7 | 914 ab |
| Astarte | 1232.2 | 995.2 | 2023.2 | 919.2 | 708.6 | 691.6 | 1095 a |
| Karnico | 1045.7 | 795.8 | 1811.1 | 836.5 | – | – | 1122 a |
| Mean† | 1194 a | 893 b | 1183 a | 852 c | 813 d | 680 e | |
| F1 mean‡ | 1331 a | 948 d | 1076 c | 904 e | 1159 b | 722 f | |

**Table 2.2.** (Continued)

| Parameter | Exp. 1 | Exp. 2 | Exp. 3 | Exp. 4 | Exp. 5 | Exp. 6 | Mean¶ |
|---|---|---|---|---|---|---|---|
| $A_2$ (*td %*) | | | | | | | |
| SH | 1130 | 1361 | 1394 | 978 | 2091 | 2288 | 1540 d |
| RH | 797 | 610 | 326 | 1454 | 3296 | 1380 | 1311 d |
| Première | 1498 | 623 | 966 | 1323 | 2267 | 2558 | 1539 d |
| Bintje | 1373 | 1627 | 1752 | 2871 | 3472 | 2671 | 2294 c |
| Seresta | 2580 | 2789 | 3050 | 4648 | 4967 | 3806 | 3640 a |
| Astarte | 1537 | 1665 | 3171 | 4939 | 5875 | 4983 | 3695 a |
| Karnico | 807 | 926 | 4376 | 5543 | – | – | 2913 b |
| Mean† | 1389 e | 1372 e | 2148 d | 3108 b | 3661 a | 2948 c | |
| F1 mean‡ | 1050 c | 1098 c | 906 d | 2065 b | 2472 a | 2442 a | |
| $A_3$ (*td %*) | | | | | | | |
| SH | 1127.5 | 903.6 | 895.1 | 1826.9 | 859.9 | 941.9 | 1092 bc |
| RH | 971.4 | 679.9 | 910.6 | 1482 | 645.8 | 1257.8 | 991 c |
| Première | 605 | 1158.1 | 1010 | 878.1 | 1107.3 | 828.5 | 931 c |
| Bintje | 1807.5 | 1583.4 | 2185.9 | 1277.4 | 875.5 | 1065.5 | 1466 b |
| Seresta | 1196.8 | 1622 | 1545.7 | 732.8 | 588.5 | 1095.1 | 1130 bc |
| Astarte | 2445.7 | 2655.5 | 584.1 | 707.4 | 604.2 | 880 | 1313 bc |
| Karnico | 3257.6 | 3373.6 | 866.9 | 1188.4 | – | – | 2172 a |
| Mean† | 1630 b | 1711 a | 1143 c | 1156 c | 780 e | 1011 d | |
| F1 mean‡ | 1074 cd | 1286 a | 1112 bc | 1169 b | 1039 d | 1073 cd | |
| $A_{sum}$ (*td %*) | | | | | | | |
| SH | 3713 | 3457 | 3012 | 3853 | 4190 | 4015 | 3707 d |
| RH | 2715 | 2033 | 2046 | 3690 | 4552 | 3273 | 3051 e |
| Première | 3304 | 2681 | 2589 | 2979 | 4113 | 3948 | 3269 e |
| Bintje | 4412 | 3974 | 5224 | 4993 | 5104 | 4396 | 4684 c |
| Seresta | 5024 | 5273 | 5607 | 6168 | 6383 | 5647 | 5684 b |
| Astarte | 5215 | 5316 | 5778 | 6566 | 7188 | 6555 | 6103 a |
| Karnico | 5110 | 5095 | 7054 | 7568 | – | – | 6207 a |
| Mean† | 4213 e | 3976 f | 4473 d | 5116 b | 5255 a | 4639 c | |
| F1 mean‡ | 3455 d | 3332 e | 3094 f | 4138 c | 4685 a | 4246 b | |

Means followed by different letters are significantly different according to Fisher's Multiple Range Test ($P$<0.05).

¶Genotype (two parents and four or five cultivars) mean across six experiments (i.e. environments).

† Mean of each individual environment across genotypes (two parents and four or five cultivars).

‡ F1 mean of each individual environment across F1 population (100 genotypes).

$t_{m1}$: LSD for genotype = 1.6; LSD for environment = 0.3; LSD for G×E = 2.8
$t_1$: LSD for genotype = 3.0; LSD for environment = 0.5; LSD for G×E = 5.1
$t_2$: LSD for genotype = 5.5; LSD for environment = 0.9; LSD for G×E = 9.6
$t_e$: LSD for genotype = 4.0; LSD for environment = 0.7; LSD for G×E = 6.9
$v_{max}$: LSD for genotype = 4.9; LSD for environment = 0.8; LSD for G×E = 8.5
$c_{m1}$: LSD for genotype = 1.3; LSD for environment = 0.2; LSD for G×E = 2.3
$c_1$: LSD for genotype = 0.5; LSD for environment = 0.1; LSD for G×E = 0.9
$c_3$: LSD for genotype = 2.7; LSD for environment = 0.5; LSD for G×E = 4.8
$D_{P2}$: LSD for genotype = 6.1; LSD for environment = 1.0; LSD for G×E = 10.6
$D_{P3}$: LSD for genotype = 6.6; LSD for environment = 1.1; LSD for G×E = 11.5
$A_1$: LSD for genotype =224.1; LSD for environment = 37.2; LSD for G×E = 388.1
$A_2$: LSD for genotype = 568.2; LSD for environment = 94.3; LSD for G×E = 984.2
$A_3$: LSD for genotype = 392.7; LSD for environment = 65.2; LSD for G×E = 680.2
$A_{sum}$: LSD for genotype = 386.4; LSD for environment = 64.1; LSD for G×E = 669.2

the differences were not large. These rates were comparatively higher for early maturing cultivars than those maturing late. Average senescence rate during *P*3 (i.e. $c_3$) was not sensitive to the maturity type of the genotypes.

The total biomass production and accumulation of potato cultivars are dependent on the intercepted PAR (Spitters, 1988; Vos and Groenwold, 1989; Van Delden, 2001). The amount of light intercepted is in proportion to the area under the whole canopy curve (Vos, 1995b). Mean estimates for $A_{sum}$ ranged from 3051 to 6207 *td* % for five standard cultivars and two parental genotypes. $A_{sum}$ values were higher for late cultivars like Karnico and Astarte than for early cultivars such as Première (Table 2.2). The area under canopy cover during *P*2, i.e. $A_2$, significantly contributed to the higher values of $A_{sum}$ in late cultivars (Table 2.2). Mean values of $A_{sum}$ also showed highly significant ($P<0.05$) variation within the F1 population across the six environments (Table 2.2).

The variation (the median, minimum and maximum values) of these model parameters and secondary derived secondary traits for the F1 population per individual experiment is illustrated in Figs. 2.3 and 2.4, respectively. The ranges of the

five model parameters were consistently wider in Exp 3 than in the other experiments (Fig. 2.3). In case of growth rates (i.e. $c_{m1}$, $c_1$, and $c_3$) wider ranges were observed in Exps 4 and 5 (Fig. 2.4). Wide ranges of variation were observed for duration of the three phases of canopy development i.e. $t_1$ in Exp 3, for $D_{P2}$ in Exp 4, and for $D_{P3}$ in Exp 2. In the case of the areas under the curves, the ranges within the population were largest in Exp 3 for $A_1$, in Exps 4 and 5 for $A_2$, and in Exp 2 for $A_3$. For $A_{sum}$, the ranges were highest in Exp 3 and values were between 1030 and 6101 *td* % (Fig. 2.4). These results were in line with the results for the length of three phases $t_1$, $D_{P2}$, and $D_{P3}$. Within the F1 population, some genotypes particularly SHRH34-H6, SHRH83-L9, and SHRH-136) recorded the highest average $A_{sum}$ with values (6146, 5836, and 5739 *td*%, respectively). This shows that genotypes like these may have higher potential to intercept the PAR and tuber yield production. Most of the parameters were nearly normally distributed (Figs. 2.5 and 2.6) which might indicate their transgressive segregation.

### 3.3. *Phenotypic, genetic and environmental variances*

Table 2.3 presents estimated values of phenotypic, genetic, and environmental variances for all the parameters and the derived secondary traits in the F1 population. The results revealed considerable phenotypic and genetic variances for the traits. Almost all the components of variation were significant ($P$<0.01) (Table 2.3).

The major portion of the phenotypic variance was accounted for by the genetic variance component for $t_2$, $t_e$, and $A_{sum}$ (Table 2.3). The contribution of the environmental variance to the phenotypic variance was relatively large for $t_{m1}$, $t_1$, $v_{max}$, and the derived secondary traits $c_{m1}$, $c_1$, $c_3$, $D_{P2}$, and $A_2$. The contribution of the G×E interaction variance component to the phenotypic variance was large for traits $D_{P3}$, $A_1$, and $A_3$ (Table 2.3).

Estimates of phenotypic ($CV_{Ph}$) and genetic ($CV_G$), environmental ($CV_E$), and G×E interaction ($CV_{GE}$) coefficients of variation for model parameters and derived secondary traits across the six experiments are presented in Table 2.4. Estimates of $CV_{Ph}$ ranged from 15.4% to 69.4%. These estimates were smallest for $t_e$ and $v_{max}$ and highest for $D_{P2}$ and $A_2$. Traits with higher $CV_{Ph}$ exhibit more total variance and are useful as selection criteria in breeding provided the trait is also heritable. Our F1 population reflected high $CV_G$ for almost all traits except for $t_{m1}$, $t_1$, $v_{max}$, and $A_1$. Relatively higher $CV_G$ and lower $CV_E$ estimates were obtained for $t_2$, $t_e$, $A_3$, and $A_{sum}$ suggesting that these traits, compared with the other ones, are under a greater influence of genetic control. The $CV_E$ was comparatively higher than $CV_G$ for traits $t_{m1}$,

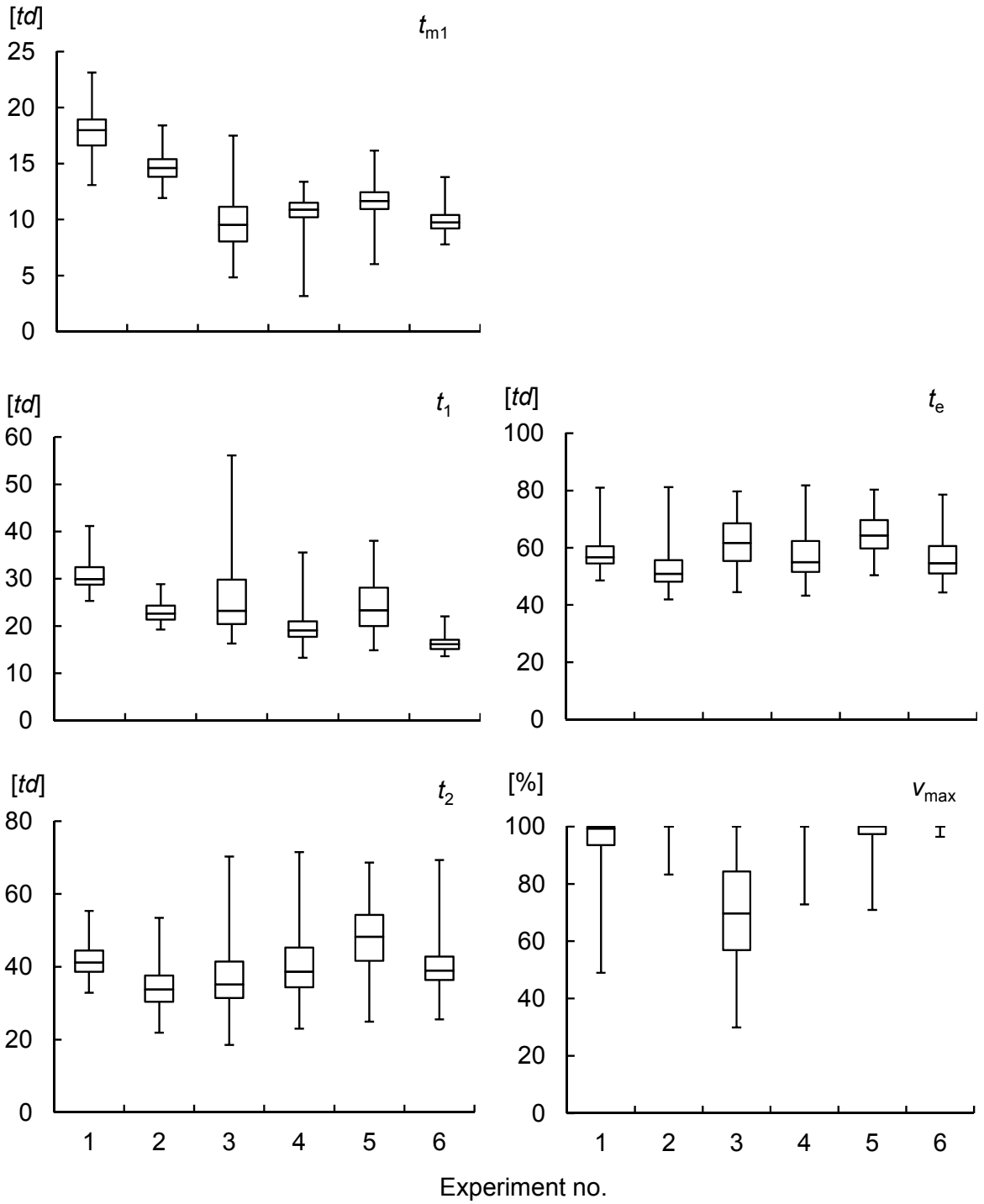


**Figure 2.3.** Box plots of genetic means of an F1 population for five model parameters in all six experiments. The boxes span the interquartile range of the trait values, so that the middle 50% of the data lay within the box, with a horizontal line indicating the median. Whiskers extend beyond the ends of the box as far as the minimum and maximum values.

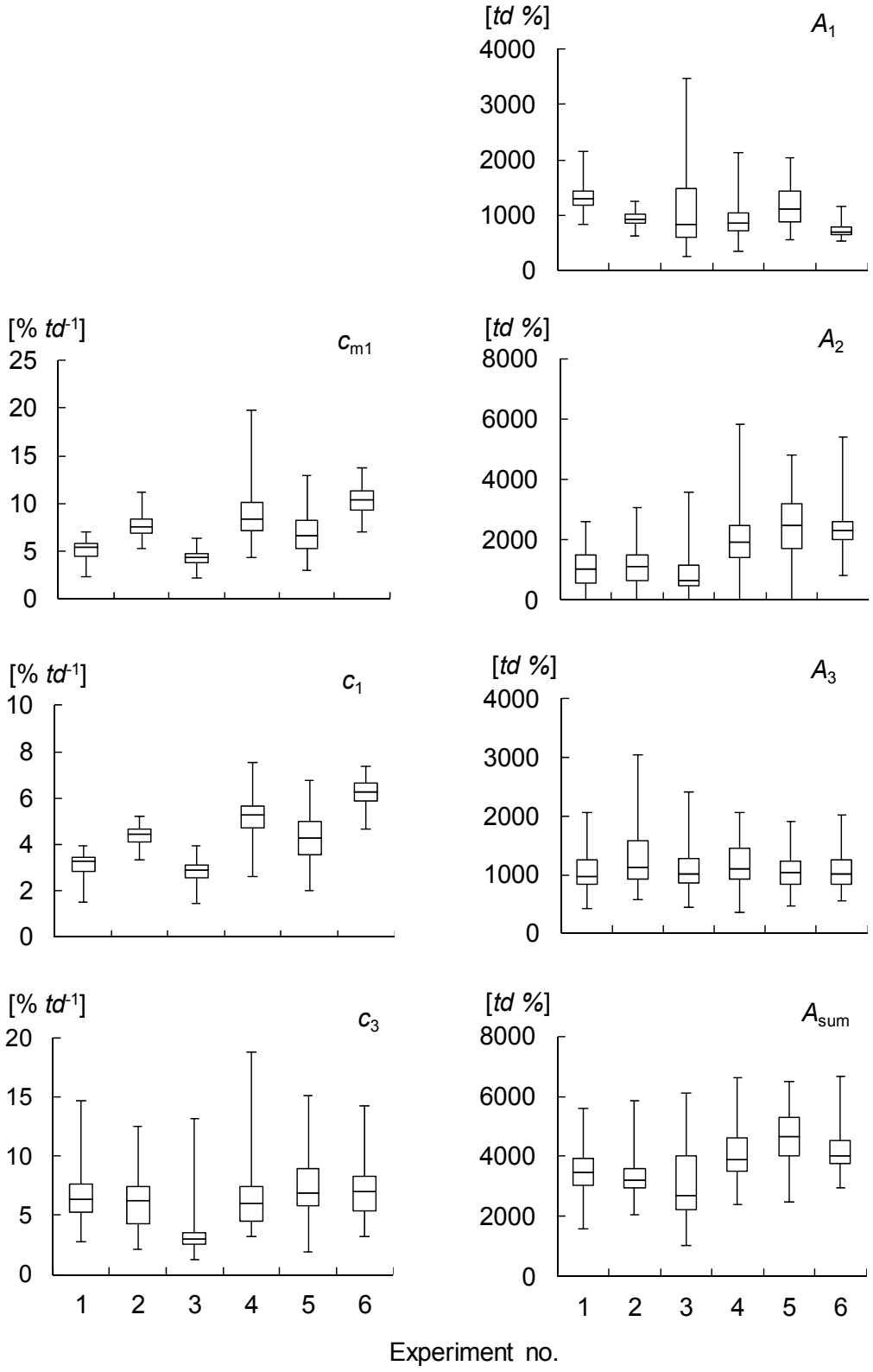


**Figure 2.4.** Box plots of genetic means of an F1 population for seven secondary derived traits in all six experiments. The boxes span the interquartile range of the trait values, so that the middle 50% of the data lay within the box, with a horizontal line indicating the median. Whiskers extend beyond the ends of the box as far as the minimum and maximum values.

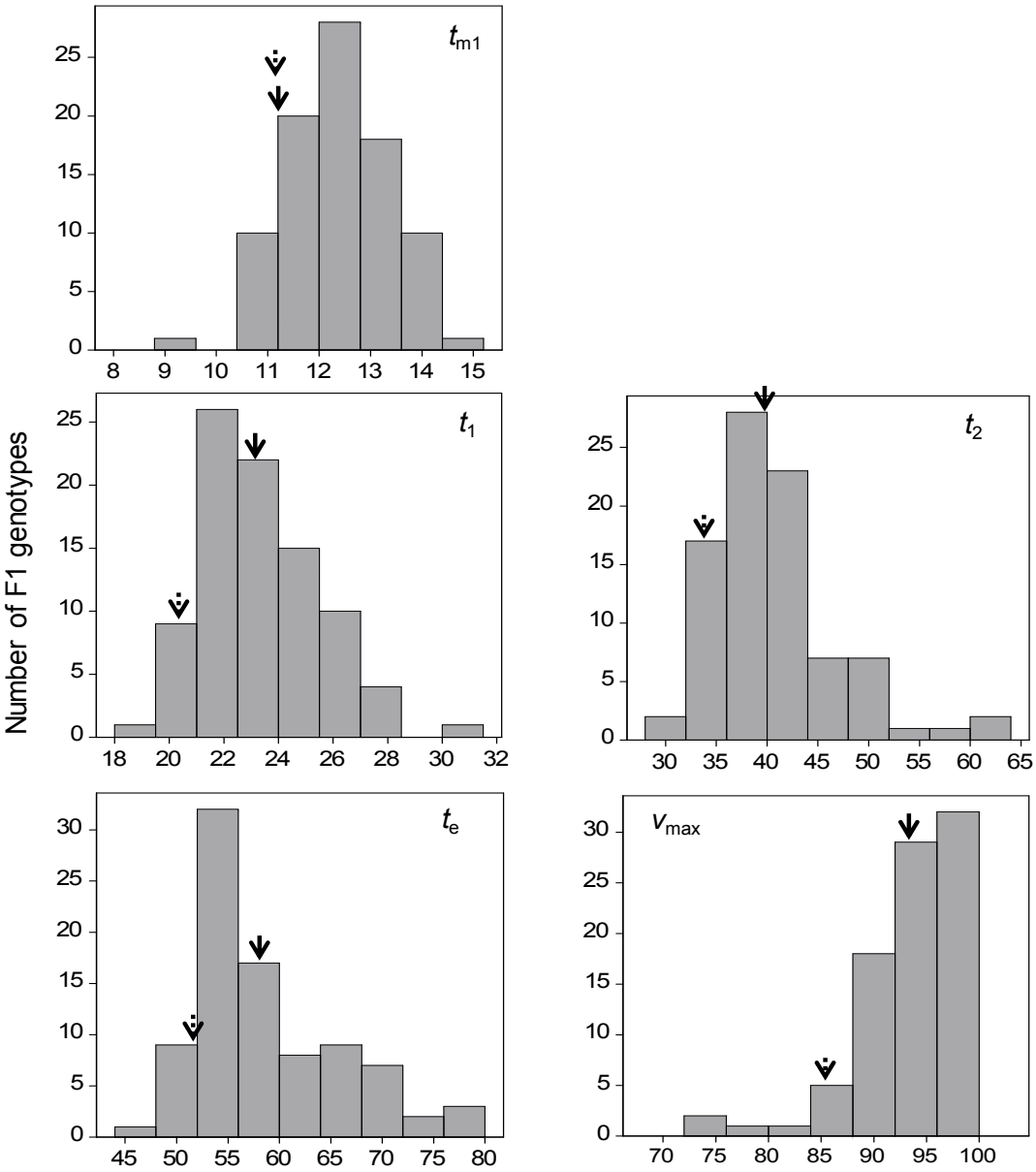


**Figure 2.5.** Distribution of five model parameters among F1 genotypes across six experiments. The values of two parents 'SH' and 'RH' are indicated by full arrow and dashed arrow, respectively.

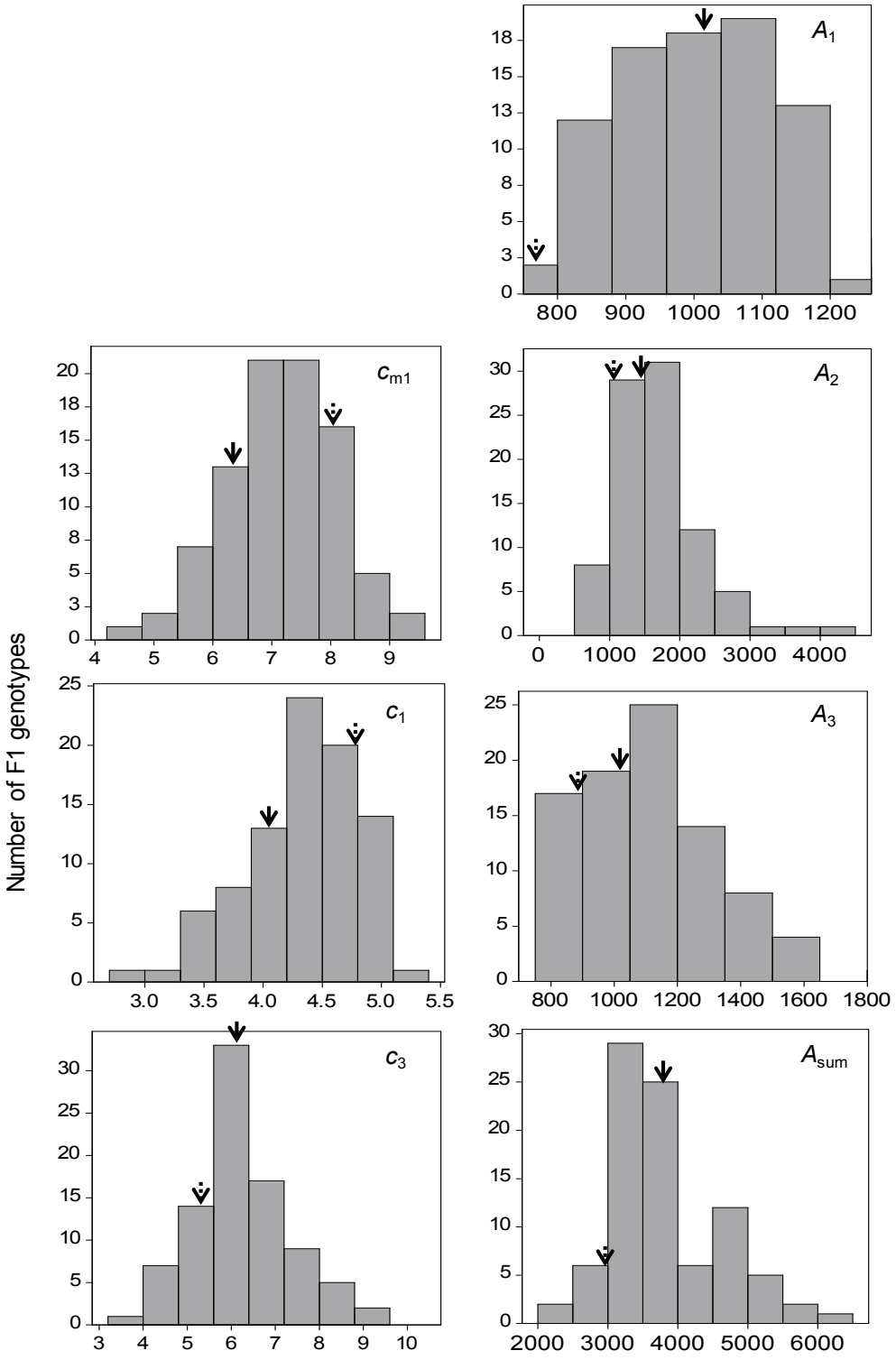


**Figure 2.6.** Distribution of seven secondary derived traits among F1 genotypes across six experiments. The values of two parents 'SH' and 'RH' are indicated by full arrow and dashed arrow, respectively.

**Table 2.3.** Variance components for five model parameters ($t_{m1}$, $t_1$, $t_2$, $t_e$, $v_{max}$) and nine derived secondary traits ($c_{m1}$, $c_1$, $c_3$, $D_{P2}$, $D_{P3}$, $A_1$, $A_2$, $A_3$, $A_{sum}$) within the F1 population across all six experiments.

| Parameter | $\sigma^2_{ph}$ | $\sigma^2_E$ | $\sigma^2_\beta$ | $\sigma^2_G$ | $\sigma^2_{GE}$ | $\sigma^2_\varepsilon$ |
|---|---|---|---|---|---|---|
| $t_{m1}$ ($td$) | 14.4 | 10.7** | 0.1** | 0.5** | 1.2** | 1.9 |
| $t_1$ ($td$) | 47.8 | 25.1** | 0.5** | 1.7** | 13.6** | 6.9 |
| $t_2$ ($td$) | 98.0 | 22.8** | 2.1** | 36.2** | 13.7** | 23.2 |
| $t_e$ ($td$) | 88.2 | 15.4** | 0.9** | 54.1** | 6.3** | 11.5 |
| $v_{max}$ (%) | 207.6 | 124.9** | 0.2$^{NS}$ | 16.9** | 45.7** | 19.9 |
| $c_{m1}$ (% $td^{-1}$) | 8.4 | 4.9** | 0.4** | 0.6** | 1.0** | 1.4 |
| $c_1$ (% $td^{-1}$) | 2.2 | 1.5** | 0.1** | 0.2** | 0.2** | 0.2 |
| $c_3$ (% $td^{-1}$) | 9.6 | 1.9** | 0.1** | 0.3** | 1.5** | 5.8 |
| $D_{P2}$ ($td$) | 128.5 | 44.3** | 2.2** | 33.5** | 19.9** | 28.6 |
| $D_{P3}$ ($td$) | 59.9 | 8.4* | 2.5** | 5.1** | 11.6** | 32.3 |
| $A_1$ ($td$ %) | 166690 | 42225** | 3096** | 0.0[1] | 81689** | 39680 |
| $A_2$ ($td$ %) | 1348961 | 527517** | 13971** | 376931** | 184725** | 245817 |
| $A_3$ ($td$ %) | 197626 | 4618$^{NS}$ | 4557** | 30015** | 44409** | 114027 |
| $A_{sum}$ ($td$ %) | 1206327 | 372964** | 9647** | 611003** | 99925** | 112788 |

** Significant at 1%, * Significant at 5%, $^{NS}$ Non-significant.

[1] The variance estimate was negative so assumed zero.

$\sigma^2_{Ph}$ = phenotypic variance, $\sigma^2_{ß}$ = block variance, $\sigma^2_G$ = genetic variance, $\sigma^2_E$ = environmental variance, $\sigma^2_{GE}$ = genotype × environmental interaction variance, $\sigma^2_\varepsilon$ = residual variance.

$t_1$, $v_{max}$, $c_{m1}$, $c_1$, $c_3$, $D_{P2}$, $D_{P3}$, and $A_2$, thus reflect environmental sensitivity of these traits. The $CV_{GE}$ ranged from 4.3% to 28.0% among the traits. The results further showed that $CV_{GE}$ exceeded the $CV_G$ for traits $t_{m1}$, $t_1$, $v_{max}$, $c_{m1}$, $c_3$, $D_{P3}$, and $A_3$. These results show the major contribution of G×E to the $CV_{Ph}$ of these traits in our experiments. It is normally difficult to select for traits that are sensitive to environmental factors. However, our results indicated that overall considerable genetic variability existed for most traits which could be exploited for improvement of light interception efficiency.

**Table 2.4.** The phenotypic coefficient of variation ($CV_{Ph}$%), genetic coefficient of variation ($CV_G$%), environmental coefficient of variation ($CV_E$%), and G×E interaction coefficient of variation ($CV_{GE}$%) for five model parameters ($t_{m1}$, $t_1$, $t_2$, $t_e$, $v_{max}$) and nine derived secondary traits ($c_{m1}$, $c_1$, $c_3$ , $D_{P2}$, $D_{P3}$, $A_1$, $A_2$, $A_3$, $A_{sum}$) within the F1 population across all six experiments.

| Parameter | Mean¶ | $CV_{Ph}$ | $CV_G$ | $CV_E$ | $CV_{GE}$ |
|---|---|---|---|---|---|
| $t_{m1}$ ($td$) | 12.4 | 30.5 | 5.7 | 26.3 | 8.8 |
| $t_1$ ($td$) | 23.3 | 29.7 | 5.6 | 21.5 | 15.8 |
| $t_2$ ($td$) | 40.7 | 24.3 | 14.8 | 11.7 | 9.1 |
| $t_e$ ($td$) | 59.0 | 15.9 | 12.5 | 6.7 | 4.3 |
| $v_{max}$ (%) | 93.6 | 15.4 | 4.4 | 11.9 | 7.2 |
| $c_{m1}$ (% $td^{-1}$) | 7.2 | 40.3 | 10.8 | 30.9 | 14.2 |
| $c_1$ (% $td^{-1}$) | 4.3 | 33.9 | 9.6 | 28.7 | 9.4 |
| $c_3$ (% $td^{-1}$) | 6.2 | 50.4 | 9.3 | 22.3 | 19.7 |
| $D_{P2}$ ($td$) | 17.4 | 65.1 | 33.3 | 38.3 | 25.6 |
| $D_{P3}$ ($td$) | 18.4 | 42.1 | 12.3 | 15.8 | 18.5 |
| $A_1$ ($td$ %) | 1021 | 40.0 | 0.0 | 20.1 | 28.0 |
| $A_2$ ($td$ %) | 1674 | 69.4 | 36.7 | 43.4 | 25.7 |
| $A_3$ ($td$ %) | 1129 | 39.4 | 15.3 | 6.0 | 18.7 |
| $A_{sum}$ ($td$ %) | 3801 | 28.9 | 20.6 | 16.1 | 8.3 |

¶Grand mean of the F1 segregating population across all six experiments.

### 3.4. *GGE biplot analysis*

Here we discuss only the results for trait $t_1$, which had both a strong G and GE component. The GGE biplots revealed that the 1st and the 2nd principal components accounted for 85.84% of the G×E variation (Fig. 2.7). The environment vectors covered a wide range of Euclidean space, indicating the existence of strong G×E interactions among the six environments evaluated.

The results were further analysed for uniqueness of environments. As shown by Fig. 2.7, four environments (Exps 1, 2, 4, and 6) were grouped together. This suggests that these environments were highly correlated and relatively similar in the manner

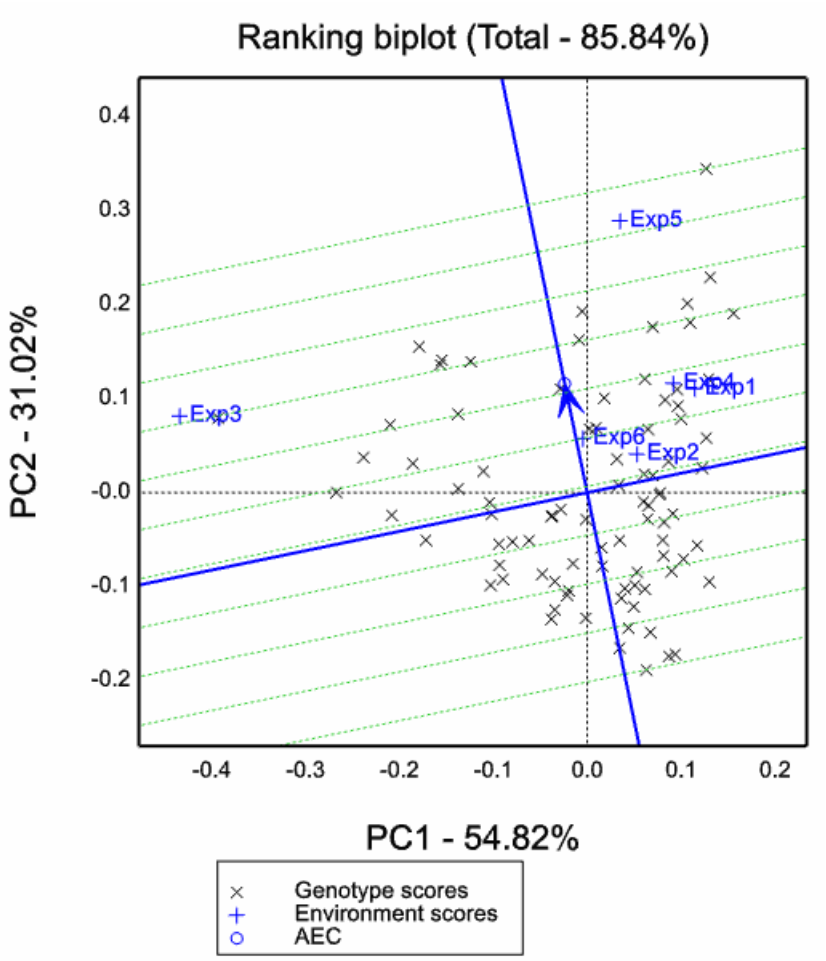


**Figure 2.7.** GGE biplot chart showing relationships among six experiments (environments) for model parameter $t_1$ in an F1 segregating population. AEC indicates average environment coordinate (Yan, 2001; Yan and Kang, 2003). A line that passes through the biplot origin and average environment indicates the mean performance of genotypes.

they discriminate among genotypes. For any particular environment, genotypes can be compared by projecting a perpendicular from the genotype symbols to the environment vector, i.e. genotypes that are further along in the positive direction of the environment vector are better performing and vice versa. The greater the distance from the origin to the intersection of a genotype projection on an environment vector, the more this genotype deviates from the average in this environment (Kroonenberg, 1997; Chapman et al., 1997). The results showed that environments (Exps 2 and 6) fell close to the origin. This could mean that these

environments may have little variability across genotypes (Kroonenberg, 1997). However, marker of environment (Exp 3) was standing furthest apart from the origin which may suggest that this environment caused maximum variability across the genotypes. These results are in line with our earlier described results that Exp 3 caused the maximum variability for some traits. This environment might therefore be the main contributor to the overall G×E on account of its lowest N availability than the rest of the environments. It would not be expected that the same genotype would be the most effective in most of the environments and therefore a focus on why particular genotypes perform exceptionally well in either low or high input situations could enable selection strategies to be developed for improved varieties. This analysis therefore allowed a partial understanding of the environmental causes of the observed G×E interaction.

### 3.5. *Phenotypic correlations of model parameters and the secondary traits*

Table 2.5 illustrates the phenotypic correlation coefficients among all the traits within the F1 population. The results showed variation in the relationship across individual experiments. For the case of the five model parameters, there were weak correlations ($r \leq 0.50$) between $t_{m1}$ and $t_{1,}$ and between $t_1$ and $t_2$ in most experiments, but not in Exps 2 and 3, where moderate positive correlations were found. There were stronger positive correlations ($r \geq 0.80$) between $t_2$ and $t_e$ in Exps 3, 4, 5, and 6. Exps 1 and 2, however, showed moderate ($r = 0.63$) to low ($r = 0.44$) $t_2$-$t_e$ correlations, respectively (Table 2.5). The results further showed little phenotypic correlation between the thermal days required for the different phases and the maximum soil cover: $t_{m1}$-$v_{max}$, $t_1$-$v_{max}$, $t_2$-$v_{max}$, and $t_e$-$v_{max}$. Only Exp 3 showed positive strong correlations with $r$ = 0.51, 0.79, 0.69, 0.69, respectively (Table 2.5).

There were strong negative phenotypic correlations between growth rates ($c_{m1}$ and $c_1$) and $t_1$ and between $c_3$ and $D_{P3}$, which suggests a trade-off between rate and duration of the canopy build-up and senescence, respectively (Table 2.5). The results further showed strong negative correlations between $t_1$ and $D_{P2}$ in several experiments. The correlations between $D_{P2}$ and $D_{P3}$ were mostly weak and non-significant, only Exps 3 and 4 showed significant ($P<0.05$) and strong ($r$ = -0.59) negative correlations (Table 2.5). These results suggest that genotypes with slow canopy build-up had a relatively short period of maximum canopy cover ($D_{P2}$). Furthermore, $t_1$ and $D_{P2}$ also depended upon $v_{max}$, with $t_1$ generally being long with a low $v_{max}$ but with $D_{P2}$ generally being short when $v_{max}$ was below 100%, whereas $D_{P2}$ could be (much) longer when the canopy reached 100% cover. The results further revealed strong positive correlations between $D_{P2}$ and $t_e$, whereas in half of the

experiments $D_{P3}$ and $t_e$ were positively correlated. This suggests that both $D_{P2}$ and $D_{P3}$ contribute positively to higher values of $t_e$. Later cultivars tended to senesce more slowly (i.e. tended to have a longer $D_{P3}$) than earlier cultivars. The results showed weak correlations between $A_1$, $A_2$, and $A_3$ (Table 2.5). The correlation coefficient ranged from −0.03 to 0.44. These results are in line with those for $t_1$, $D_{P2}$, and $D_{P3}$. There was a strong, positive correlation between $A_2$ and $A_{sum}$ in all experiments, underlining the important contribution of variation in $A_2$ to variation in $A_{sum}$.

In short, our results suggest a large complexity of the genetic and physiological inter-relations between the various model parameters and derived secondary traits.

### 3.6. *Genetic correlations of model parameters and the secondary traits*

Table 2.5 illustrates the genetic correlation coefficients between the model parameters and secondary traits within the F1 population. The results showed weak ($r \leq 0.50$) genetic correlations between $t_{m1}$ and $t_1$ in Exps 4 and 5, and between $t_1$ and $t_2$ in all experiments except Exp 2. The other experiments showed positive and strong ($r > 0.50$) $t_{m1}$-$t_1$ and $t_1$-$t_2$ genetic correlations. Positive genetic correlations between $t_2$ and $t_e$ were strong in all experiments (Table 2.5). There was little genetic correlation between the thermal days required for the different phases and the maximum soil cover: $t_{m1}$-$v_{max}$, $t_1$-$v_{max}$, $t_2$-$v_{max}$, and $t_e$-$v_{max}$ showed poor correlations. However, these correlations were stronger and positive in Exp 3 with $r$ = 0.59, 0.87, 0.75, 0.75, respectively (Table 2.5). There were strong negative genetic correlations between growth rates ($c_{m1}$ and $c_1$) and $t_1$ and between $c_3$ and $D_{P3}$.

The results further revealed weak genetic correlations between $t_1$ and $D_{P2}$ in Exps 2, 3, and 6, whereas Exps 1, 4, and 5 showed strong negative correlations (Table 2.5). The genetic correlations between $D_{P2}$ and $D_{P3}$ were mostly weak and non-significant, only Exp 5 showed significant a negative genetic correlation with $r$ = -0.79. There were strong positive genetic correlations between $D_{P2}$ and $v_{max}$ in all the experiments except in Exps 3 and 6. The trait $D_{P2}$ also showed strong positive genetic correlations with $t_e$ in all experiments. About half of experiments also showed strong positive genetic correlations between $D_{P3}$ and $t_e$. These results indicate that genotypes with longer $D_{P2}$ and $D_{P3}$ could be indirectly obtained by selecting genotypes with high $v_{max}$ and $t_e$.

There were weak genetic correlations between $A_1$ and $A_2$, and between $A_2$ and $A_3$ in most experiments. However, there were strong positive genetic correlations between $A_2$ and $A_{sum}$ in all experiments and between $A_3$ and $A_{sum}$ in half of the experiments (Table 2.5). These results are in line with those for $t_1$, $D_{P2}$, and $D_{P3}$ and highlight the importance of both $A_2$ and $A_3$ to be used as an indirect selection measure

**Table 2.5.** Phenotypic (lower triangle) and genetic (upper triangle) correlation coefficients among all pair wise comparisons of five model parameters ($t_{m1}$, $t_1$, $t_2$, $t_e$, $v_{max}$) and nine derived secondary traits ($c_{m1}$, $c_1$, $c_3$, $D_{P2}$, $D_{P3}$, $A_1$, $A_2$, $A_3$, $A_{sum}$) within the F1 population per individual experiment. The unit for all model parameters is thermal day (*td*) except for $v_{max}$ (%) and the derived traits $A_1$, $A_2$, $A_3$, $A_{sum}$ (*td* %) and $c_{m1}$, $c_1$, $c_3$ (% $td^{-1}$).

| | $t_{m1}$ | $t_1$ | $t_2$ | $t_e$ | $v_{max}$ | $c_{m1}$ | $c_1$ | $c_3$ | $D_{P2}$ | $D_{P3}$ | $A_1$ | $A_2$ | $A_3$ | $A_{sum}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Exp. 1*** | | | | | | | | | | | | | | |
| $t_{m1}$ | | 0.56** | -0.13$^{NS}$ | -0.12$^{NS}$ | -0.11$^{NS}$ | -0.27** | -0.40** | -0.03$^{NS}$ | -0.38** | -0.05$^{NS}$ | 0.21* | -0.36** | -0.10$^{NS}$ | -0.30** |
| $t_1$ | 0.43** | | -0.44** | -0.41** | -0.60** | -0.91** | -0.92** | -0.10$^{NS}$ | -0.82** | -0.20* | 0.71** | -0.82** | -0.39** | -0.70** |
| $t_2$ | -0.02$^{NS}$ | -0.30** | | 0.78** | 0.43** | 0.53** | 0.50** | 0.07$^{NS}$ | 0.88** | 0.21* | -0.23* | 0.87** | 0.30** | 0.82** |
| $t_e$ | -0.07$^{NS}$ | -0.38** | 0.62** | | 0.37** | 0.51** | 0.48** | -0.52** | 0.72** | 0.78** | -0.27** | 0.72** | 0.80** | 0.88** |
| $v_{max}$ | -0.09$^{NS}$ | -0.48** | 0.35** | 0.32** | | 0.85** | 0.87** | 0.26** | 0.60** | 0.15$^{NS}$ | 0.04$^{NS}$ | 0.62** | 0.48** | 0.73** |
| $c_{m1}$ | -0.07$^{NS}$ | -0.85** | 0.42** | 0.47** | 0.75** | | 0.98** | 0.15$^{NS}$ | 0.83** | 0.27** | -0.50** | 0.84** | 0.52** | 0.82** |
| $c_1$ | -0.32** | -0.88** | 0.40** | 0.44** | 0.83** | 0.94** | | 0.17$^{NS}$ | 0.81** | 0.25* | -0.41** | 0.82** | 0.51** | 0.82** |
| $c_3$ | 0.02$^{NS}$ | -0.02$^{NS}$ | 0.30** | -0.47** | 0.23* | 0.10$^{NS}$ | 0.12$^{NS}$ | | 0.10$^{NS}$ | -0.88** | 0.12$^{NS}$ | 0.10$^{NS}$ | -0.69** | -0.17$^{NS}$ |
| $D_{P2}$ | -0.24* | -0.75** | 0.86** | 0.64** | 0.51** | 0.75** | 0.75** | 0.22* | | 0.24* | -0.52** | 1.00** | 0.40** | 0.90** |
| $D_{P3}$ | -0.08$^{NS}$ | -0.21* | -0.12$^{NS}$ | 0.70** | 0.09$^{NS}$ | 0.20$^{NS}$ | 0.20* | -0.86** | 0.03$^{NS}$ | | -0.20$^{NS}$ | 0.25** | 0.95** | 0.55** |
| $A_1$ | -0.05$^{NS}$ | 0.70** | -0.14$^{NS}$ | -0.24* | 0.13$^{NS}$ | -0.53** | -0.37** | 0.13$^{NS}$ | -0.48** | -0.18$^{NS}$ | | -0.52** | -0.15$^{NS}$ | -0.27** |
| $A_2$ | -0.24* | -0.75** | 0.85** | 0.65** | 0.55** | 0.77** | 0.78** | 0.21* | 1.00** | 0.04$^{NS}$ | -0.46** | | 0.42** | 0.91** |
| $A_3$ | -0.10$^{NS}$ | -0.33** | -0.01$^{NS}$ | 0.74** | 0.38** | 0.41** | 0.43** | -0.74** | 0.17$^{NS}$ | 0.95** | -0.11$^{NS}$ | 0.20* | | 0.72** |
| $A_{sum}$ | -0.28** | -0.62** | 0.72** | 0.85** | 0.70** | 0.73** | 0.79** | -0.11$^{NS}$ | 0.84** | 0.43** | -0.17$^{NS}$ | 0.86** | 0.61** | |

** Significant at 1%, * Significant at 5%, $^{NS}$ Non-significant.

**Table 2.5.** (Continued)

| | $t_{m1}$ | $t_1$ | $t_2$ | $t_e$ | $v_{max}$ | $c_{m1}$ | $c_1$ | $c_3$ | $D_{P2}$ | $D_{P3}$ | $A_1$ | $A_2$ | $A_3$ | $A_{sum}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Exp. 2*** | | | | | | | | | | | | | | |
| $t_{m1}$ | | 0.82** | 0.08 NS | -0.10 NS | -0.45** | -0.40** | -0.76** | 0.23* | -0.21* | -0.18 NS | 0.47** | -0.21* | -0.18 NS | -0.21* |
| $t_1$ | 0.69** | | -0.10 NS | -0.43** | -0.78** | -0.86** | -0.99** | 0.42** | -0.42** | -0.46** | 0.89** | -0.43** | -0.46** | -0.51** |
| $t_2$ | 0.05 NS | -0.11 NS | | 0.58** | 0.48** | 0.16 NS | 0.13 NS | 0.06 NS | 0.94** | 0.04 NS | -0.14 NS | 0.94** | 0.05 NS | 0.72** |
| $t_e$ | -0.07 NS | -0.31** | 0.45** | | 0.46** | 0.48** | 0.45** | -0.75** | 0.67** | 0.84** | -0.53** | 0.66** | 0.85** | 0.97** |
| $v_{max}$ | -0.16 NS | -0.34** | 0.21* | 0.25* | | 0.76** | 0.85** | -0.19 NS | 0.69** | 0.25** | -0.75** | 0.71** | 0.27** | 0.60** |
| $c_{m1}$ | -0.25** | -0.84** | 0.15 NS | 0.35** | 0.41** | | 0.89** | -0.39** | 0.43** | 0.49** | -1.00** | 0.44** | 0.49** | 0.52** |
| $c_1$ | -0.66** | -0.97** | 0.13 NS | 0.33** | 0.52** | 0.87** | | -0.40** | 0.45** | 0.46** | -0.89** | 0.46** | 0.47** | 0.53** |
| $c_3$ | 0.17 NS | 0.22* | 0.26** | -0.64** | -0.05 NS | -0.18 NS | -0.20* | | -0.08 NS | -0.96** | 0.47** | -0.08 NS | -0.97** | -0.62** |
| $D_{P2}$ | -0.19 NS | -0.45** | 0.94** | 0.52** | 0.30** | 0.43** | 0.45** | 0.16 NS | | 0.19 NS | -0.43** | 1.00** | 0.20* | 0.82** |
| $D_{P3}$ | -0.12 NS | -0.27** | -0.20 NS | 0.78** | 0.13 NS | 0.28** | 0.27** | -0.89** | -0.09 NS | | -0.55** | 0.19 NS | 1.00** | 0.71** |
| $A_1$ | 0.26** | 0.86** | -0.14 NS | -0.33** | -0.15 NS | -0.93** | -0.80** | 0.17 NS | -0.43** | -0.26** | | -0.44** | -0.56** | -0.55** |
| $A_2$ | -0.20 NS | -0.45** | 0.94** | 0.52** | 0.31** | 0.43** | 0.46** | 0.16 NS | 1.00** | -0.09 NS | -0.43** | | 0.20* | 0.82** |
| $A_3$ | -0.12 NS | -0.27** | -0.19 NS | 0.79** | 0.18 NS | 0.29** | 0.29** | -0.89** | -0.08 NS | 1.00** | -0.25* | -0.07 NS | | 0.72** |
| $A_{sum}$ | | 0.82** | 0.08 NS | -0.10 NS | -0.45** | -0.40** | -0.76** | 0.23* | -0.21* | -0.18 NS | 0.47** | -0.21* | -0.18 NS | -0.21* |

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

**Table 2.5.** (Continued)

| | $t_{m1}$ | $t_1$ | $t_2$ | $t_e$ | $v_{max}$ | $c_{m1}$ | $c_1$ | $c_3$ | $D_{P2}$ | $D_{P3}$ | $A_1$ | $A_2$ | $A_3$ | $A_{sum}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Exp. 3*** | | | | | | | | | | | | | | |
| $t_{m1}$ | | 0.64** | 0.69** | 0.62** | 0.59** | -0.55** | -0.32** | 0.76** | 0.35** | -0.33** | 0.57** | 0.57** | 0.26** | 0.65** |
| $t_1$ | 0.40** | | 0.85** | 0.77** | 0.87** | -0.65** | -0.39** | 0.94** | 0.15 NS | -0.42** | 0.99** | 0.45** | 0.56** | 0.88** |
| $t_2$ | 0.51** | 0.70** | - | 0.94** | 0.75** | -0.67** | -0.39** | 0.92** | 0.67** | -0.47** | 0.82** | 0.83** | 0.29** | 0.91** |
| $t_e$ | 0.49** | 0.69** | 0.80** | | 0.75** | -0.38** | -0.23* | 0.75** | 0.66** | -0.13 NS | 0.77** | 0.73** | 0.50** | 0.91** |
| $v_{max}$ | 0.51** | 0.79** | 0.69** | 0.69** | | -0.12 NS | 0.13 NS | 0.87** | 0.16 NS | -0.23* | 0.92** | 0.52** | 0.72** | 0.94** |
| $c_{m1}$ | -0.02 NS | -0.53** | -0.22* | -0.22* | 0.04 NS | | 1.00** | -0.45** | -0.33** | 0.81** | -0.49** | -0.23* | 0.22* | -0.29** |
| $c_1$ | 0.02 NS | -0.44** | -0.16 NS | -0.16 NS | 0.17 NS | 0.97** | | -0.16 NS | -0.19 NS | 0.46** | -0.24** | -0.04 NS | 0.30** | -0.06 NS |
| $c_3$ | 0.42** | 0.60** | 0.83** | 0.48** | 0.65** | -0.09 NS | -0.02 NS | | 0.41** | -0.79** | 0.95** | 0.77** | 0.28** | 0.92** |
| $D_{P2}$ | 0.31** | -0.03 NS | 0.69** | 0.42** | 0.17 NS | 0.22* | 0.23* | 0.56** | | -0.21* | 0.12 NS | 0.99** | -0.22* | 0.46** |
| $D_{P3}$ | -0.21* | -0.24* | -0.60** | 0.00 NS | -0.22* | 0.08 NS | 0.05 NS | -0.74** | -0.59** | | -0.35** | -0.54** | 0.50** | -0.31** |
| $A_1$ | 0.37** | 0.98** | 0.71** | 0.71** | 0.87** | -0.37** | -0.27** | 0.65** | 0.02 NS | -0.24* | | 0.45** | 0.63** | 0.90** |
| $A_2$ | 0.45** | 0.22 * | 0.83** | 0.56** | 0.47** | 0.19 NS | 0.24* | 0.74** | 0.93** | -0.63** | 0.29** | | 0.01 NS | 0.73** |
| $A_3$ | 0.18 NS | 0.37** | -0.05 NS | 0.44** | 0.54** | 0.07 NS | 0.16 NS | -0.21* | -0.44** | 0.67** | 0.43** | -0.26** | | 0.59** |
| $A_{sum}$ | 0.53** | 0.78** | 0.87** | 0.87** | 0.93** | -0.05 NS | 0.06 NS | 0.72** | 0.43** | -0.29** | 0.85** | 0.68** | 0.40** | |

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

**Table 2.5.** (Continued)

| | $t_{m1}$ | $t_1$ | $t_2$ | $t_e$ | $v_{max}$ | $c_{m1}$ | $c_1$ | $c_3$ | $D_{P2}$ | $D_{P3}$ | $A_1$ | $A_2$ | $A_3$ | $A_{sum}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Exp. 4*** | | | | | | | | | | | | | | |
| $t_{m1}$ | | -0.29** | 0.57** | 0.43** | 0.25* | 0.36** | 0.24* | 0.40** | 0.55** | -0.25** | -0.39** | 0.54** | -0.25** | 0.47** |
| $t_1$ | -0.39** | | -0.51** | -0.54** | -0.62** | -0.86** | -0.96** | 0.11 NS | -0.70** | -0.19* | 0.97** | -0.71** | -0.28** | -0.64** |
| $t_2$ | 0.28** | -0.31** | | 0.92** | 0.50** | 0.81** | 0.65** | 0.17 NS | 0.97** | 0.04 NS | -0.62** | 0.97** | 0.10 NS | 0.96** |
| $t_e$ | 0.27** | -0.37** | 0.82** | | 0.32** | 0.68** | 0.60** | -0.23* | 0.91** | 0.46** | -0.64** | 0.91** | 0.52** | 0.98** |
| $v_{max}$ | 0.20* | -0.34** | 0.29** | 0.21* | | 0.52** | 0.71** | 0.38** | 0.59** | -0.30** | -0.54** | 0.61** | -0.15 NS | 0.51** |
| $c_{m1}$ | 0.36** | -0.81** | 0.51** | 0.50** | 0.31** | | 0.89** | 0.23* | 0.90** | -0.08 NS | -0.97** | 0.90** | -0.01 NS | 0.79** |
| $c_1$ | 0.31** | -0.94** | 0.43** | 0.44** | 0.50** | 0.90** | | 0.08 NS | 0.82** | 0.04 NS | -0.94** | 0.82** | 0.13 NS | 0.72** |
| $c_3$ | 0.02 NS | 0.03 NS | 0.34** | -0.21* | 0.18 NS | 0.15 NS | 0.10 NS | | 0.11 NS | -0.95** | 0.08 NS | 0.12 NS | -0.95** | -0.07 NS |
| $D_{P2}$ | 0.36** | -0.59** | 0.95** | 0.82** | 0.36** | 0.70** | 0.67** | 0.28** | | 0.09 NS | -0.79** | 1.00** | 0.17 NS | 0.98** |
| $D_{P3}$ | 0.01 NS | -0.14 NS | -0.21* | 0.39** | -0.12 NS | 0.04 NS | 0.05 NS | -0.90** | -0.13 NS | | -0.18 NS | 0.07 NS | 0.99** | 0.29** |
| $A_1$ | -0.56** | 0.96** | -0.35** | -0.41** | -0.22* | -0.86** | -0.90** | 0.02 NS | -0.61** | -0.14 NS | | -0.79** | -0.25** | -0.73** |
| $A_2$ | 0.36** | -0.59** | 0.95** | 0.82** | 0.39** | 0.70** | 0.68** | 0.29** | 1.00** | -0.14 NS | -0.61** | | 0.15 NS | 0.97** |
| $A_3$ | 0.03 NS | -0.16 NS | -0.18 NS | 0.41** | 0.03 NS | 0.05 NS | 0.10 NS | -0.89** | -0.10 NS | 0.99** | -0.14 NS | -0.10 NS | | 0.36** |
| $A_{sum}$ | 0.26** | -0.45** | 0.91** | 0.96** | 0.40** | 0.57** | 0.56** | 0.00 NS | 0.92** | 0.17 NS | -0.46** | 0.92** | 0.22* | |

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

**Table 2.5.** (Continued)

| | $t_{m1}$ | $t_1$ | $t_2$ | $t_e$ | $v_{max}$ | $c_{m1}$ | $c_1$ | $c_3$ | $D_{P2}$ | $D_{P3}$ | $A_1$ | $A_2$ | $A_3$ | $A_{sum}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Exp. 5*** | | | | | | | | | | | | | | |
| $t_{m1}$ | | 0.12 $^{NS}$ | 0.31** | 0.40** | 0.42** | -0.18 $^{NS}$ | -0.16 $^{NS}$ | 0.18 $^{NS}$ | 0.20* | 0.05 $^{NS}$ | 0.10 $^{NS}$ | 0.21* | 0.00 $^{NS}$ | 0.32** |
| $t_1$ | 0.11 $^{NS}$ | | -0.05 $^{NS}$ | 0.05 $^{NS}$ | -0.65** | -0.99** | -1.00** | -0.56** | -0.53** | 0.30** | 0.99 $^{NS}$ | -0.52* | 0.00 $^{NS}$ | -0.26** |
| $t_2$ | 0.25* | -0.04 $^{NS}$ | | 0.97** | 0.74** | 0.11 $^{NS}$ | 0.13 $^{NS}$ | 0.79** | 0.88** | -0.75** | 0.02 $^{NS}$ | 0.88** | 0.00 $^{NS}$ | 0.99** |
| $t_e$ | 0.28** | 0.00 $^{NS}$ | 0.83** | | 0.48** | -0.06 $^{NS}$ | -0.03 $^{NS}$ | 0.72** | 0.80** | -0.60** | 0.08 $^{NS}$ | 0.80** | 0.00 $^{NS}$ | 0.93** |
| $v_{max}$ | 0.30** | -0.36** | 0.47** | 0.29** | | 0.51** | 0.61** | 1.00** | 0.94** | -1.00** | -0.54** | 0.93** | 0.00 $^{NS}$ | 0.77** |
| $c_{m1}$ | -0.13 $^{NS}$ | -0.92** | 0.07 $^{NS}$ | -0.04 $^{NS}$ | 0.40** | | 0.99** | 0.87** | 0.57** | -0.53** | -1.00** | 0.56** | 0.00 $^{NS}$ | 0.25** |
| $c_1$ | -0.13 $^{NS}$ | -0.96** | 0.10 $^{NS}$ | -0.01 $^{NS}$ | 0.49** | 0.98** | | 0.83** | 0.59** | -0.52** | -0.99** | 0.59** | 0.00 $^{NS}$ | 0.29** |
| $c_3$ | 0.13 $^{NS}$ | -0.09 $^{NS}$ | 0.54** | 0.08 $^{NS}$ | 0.37** | 0.17 $^{NS}$ | 0.18 $^{NS}$ | | 0.95** | -0.85** | -0.37** | 0.97** | 0.00 $^{NS}$ | 0.98** |
| $D_{P2}$ | 0.16 $^{NS}$ | -0.52** | 0.87** | 0.71** | 0.57** | 0.51** | 0.55** | 0.50** | | -0.79** | -0.46** | 1.00** | 0.00 $^{NS}$ | 0.97** |
| $D_{P3}$ | -0.06 $^{NS}$ | 0.07 $^{NS}$ | -0.65** | -0.11 $^{NS}$ | -0.44** | -0.17 $^{NS}$ | -0.18 $^{NS}$ | -0.86** | -0.59** | | 0.13 $^{NS}$ | -0.80** | 0.00 $^{NS}$ | -0.85** |
| $A_1$ | 0.07 $^{NS}$ | 0.97** | 0.02 $^{NS}$ | 0.03 $^{NS}$ | -0.18 $^{NS}$ | -0.91** | -0.91** | -0.03 $^{NS}$ | -0.46** | 0.00 $^{NS}$ | | -0.46** | 0.00 $^{NS}$ | -0.19 $^{NS}$ |
| $A_2$ | 0.16 $^{NS}$ | -0.52** | 0.87** | 0.71** | 0.59** | 0.51** | 0.56** | 0.50** | 1.00** | -0.58** | -0.45** | | 0.00 $^{NS}$ | 0.97 ** |
| $A_3$ | 0.00 $^{NS}$ | 0.03 $^{NS}$ | -0.58** | -0.06 $^{NS}$ | -0.20* | -0.12 $^{NS}$ | -0.10 $^{NS}$ | -0.86** | -0.51** | 0.96** | 0.01 $^{NS}$ | -0.50** | | 0.00 $^{NS}$ |
| $A_{sum}$ | 0.23* | -0.26** | 0.92** | 0.89** | 0.62** | 0.25* | 0.31** | 0.34** | 0.91** | -0.42** | -0.17 $^{NS}$ | 0.92** | -0.31** | |

** Significant at 1%, * Significant at 5%, $^{NS}$ Non-significant.

**Table 2.5.** (Continued)

| | $t_{m1}$ | $t_1$ | $t_2$ | $t_e$ | $v_{max}$ | $c_{m1}$ | $c_1$ | $c_3$ | $D_{P2}$ | $D_{P3}$ | $A_1$ | $A_2$ | $A_3$ | $A_{sum}$ |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| ***Exp. 6*** | | | | | | | | | | | | | | |
| $t_{m1}$ | | 0.71** | 0.29** | 0.29** | 0.00 NS | -0.41** | -0.72** | -0.10 NS | 0.13 NS | 0.11 NS | 0.36** | 0.13 NS | 0.13 NS | 0.20* |
| $t_1$ | 0.55 ** | | -0.03 NS | 0.24* | 0.00 NS | -0.95** | -1.00** | -0.58** | -0.24** | 0.66** | 0.91** | -0.25** | 0.67** | 0.07 NS |
| $t_2$ | 0.24* | 0.02 NS | | 0.92** | 0.00 NS | 0.16 NS | 0.02 NS | -0.13 NS | 0.98** | 0.21* | -0.18* | 0.98** | 0.21* | 0.97** |
| $t_e$ | 0.18 NS | 0.16 NS | 0.80** | | 0.00 NS | -0.14 NS | -0.23* | -0.53** | 0.84** | 0.58** | 0.16 NS | 0.84** | 0.57** | 0.98** |
| $v_{max}$ | -0.18 NS | -0.25** | 0.19 NS | 0.15 NS | | 0.00 NS | 0.00 NS | 0.00 NS | 0.00 NS | 0.00 NS | 0.00 NS | 0.00 NS | 0.00 NS | 0.00 NS |
| $c_{m1}$ | -0.20* | -0.88** | 0.11 NS | -0.06 NS | 0.26** | | 0.93** | 0.59** | 0.35** | -0.68** | -1.00** | 0.36** | -0.69** | 0.02 NS |
| $c_1$ | -0.57** | -0.99** | -0.02 NS | -0.15 NS | 0.30** | 0.89** | | 0.55** | 0.23* | -0.63** | -0.91** | 0.23* | -0.64** | -0.07 NS |
| $c_3$ | 0.05 NS | -0.22* | 0.14 NS | -0.42** | 0.04 NS | 0.24* | 0.20* | | 0.00 NS | -1.00** | -0.70** | 0.00 NS | -1.00** | -0.38** |
| $D_{P2}$ | 0.11 NS | -0.20* | 0.98** | 0.75** | 0.24* | 0.30** | 0.19* | 0.19 NS | | 0.06 NS | -0.38** | 1.00** | 0.06 NS | 0.92** |
| $D_{P3}$ | -0.04 NS | 0.23* | -0.13 NS | 0.49** | -0.03 NS | -0.26** | -0.22* | -0.91** | -0.18 NS | | 0.80** | 0.06 NS | 1.00** | 0.43** |
| $A_1$ | 0.15 NS | 0.91** | -0.09 NS | 0.10 NS | -0.17 NS | -0.96** | -0.88** | -0.28** | -0.28** | 0.29** | | -0.38** | 0.80** | -0.01 NS |
| $A_2$ | 0.11 NS | -0.20* | 0.98** | 0.75** | 0.25** | 0.30** | 0.20* | 0.18 NS | 1.00** | -0.18 NS | -0.28** | | 0.05 NS | 0.92** |
| $A_3$ | -0.03 NS | 0.25** | -0.13 NS | 0.49** | -0.01 NS | -0.27** | -0.23* | -0.91** | -0.18 NS | 1.00** | 0.30** | -0.18 NS | | 0.43** |
| $A_{sum}$ | 0.12 NS | 0.03 NS | 0.91** | 0.97** | 0.22* | 0.05 NS | -0.03 NS | -0.24* | 0.88** | 0.28** | -0.01 NS | 0.88** | 0.29** | |

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

for plants with high $A_{sum}$.

### 3.7. *Estimates of broad-sense heritability*

The estimates of broad-sense heritability ($H^2$) across six environments (eqn (2.13)) varied greatly with traits under investigation (Table 2.6). The heritability values ranged from 31.1% to 96.4%. High estimates ($H^2$ > 70%) were recorded for $t_2$, $t_e$, $c_1$, $D_{P2}$, $A_2$, and $A_{sum}$. Moderate estimates (50% < $H^2$ <70%) were recorded for $t_{m1}$, $v_{max}$, $D_{P3}$, and $A_3$ (Table 2.6). On the other hand $t_1$ and $c_3$ had a weak heritability (37.4% and 31.1%, respectively). However, highly significant genetic variation in model trait among the F1 population may offset the relatively low heritability estimates, thus making them responsive to selection. Also according to Jones et al. (1986), heritability estimates as low as 40% could be considered favourable provided that the selection techniques have enough precision. Table 2.6 also presents the estimates of broad-

**Table 2.6.** Broad-sense heritability $H^2$ (%) estimates across six experiments (eqn 2.13) and per individual experiment (eqn 2.14) for five model parameters ($t_{m1}$, $t_1$, $t_2$, $t_e$, $v_{max}$) and nine derived secondary traits ($c_{m1}$, $c_1$, $c_3$, $D_{P2}$, $D_{P3}$, $A_1$, $A_2$, $A_3$, $A_{sum}$) within the F1 population per individual experiment.

| Parameter | $H^2$† | Exp. 1 | Exp. 2 | Exp. 3 | Exp. 4 | Exp. 5 | Exp. 6 |
|---|---|---|---|---|---|---|---|
| $t_{m1}$ (*td*) | 58.3 | 59.2 | 52.5 | 68.7 | 40.8 | 74.3 | 69.2 |
| $t_1$ (*td*) | 37.4 | 79.9 | 55.7 | 89.2 | 69.5 | 77.6 | 75.6 |
| $t_2$ (*td*) | 89.6 | 70.6 | 64.6 | 86.4 | 85.6 | 79.0 | 79.8 |
| $t_e$ (*td*) | 96.4 | 89.2 | 92.1 | 92.8 | 92.0 | 85.8 | 89.4 |
| $v_{max}$ (%) | 64.6 | 88.2 | 22.9 | 92.6 | 56.5 | 46.1 | 0.0 |
| $c_{m1}$ (% $td^{-1}$) | 67.6 | 82.5 | 57.8 | 30.4 | 66.5 | 76.4 | 68.6 |
| $c_1$ (% $td^{-1}$) | 79.4 | 91.2 | 59.3 | 46.8 | 72.3 | 81.4 | 78.6 |
| $c_3$ (% $td^{-1}$) | 31.1 | 59.7 | 55.4 | 55.5 | 49.0 | 9.3 | 32.9 |
| $D_{P2}$ (*td*) | 85.5 | 82.6 | 64.4 | 54.5 | 88.6 | 80.8 | 81.2 |
| $D_{P3}$ (*td*) | 52.4 | 60.6 | 73.3 | 30.0 | 51.3 | 23.3 | 39.6 |
| $A_1$ (*td %*) | 0.0 | 57.6 | 41.3 | 93.2 | 57.6 | 70.1 | 65.5 |
| $A_2$ (*td %*) | 88.0 | 84.8 | 65.0 | 72.4 | 89.3 | 82.3 | 81.3 |
| $A_3$ (*td %*) | 64.0 | 69.2 | 73.0 | 69.1 | 48.7 | 0.0 | 41.0 |
| $A_{sum}$ (*td %*) | 95.9 | 92.3 | 90.6 | 94.9 | 94.0 | 88.1 | 92.6 |

† Broad-sense heritability across six environments.

sense heritability ($H^2$) per individual experiment (eqn (2.14)), which, in principle, should be higher than the estimates across environments, because for individual environments the genetic and G×E interaction effects are less confounded.

The high heritability estimates showed that most of the traits were little influenced by the environment and genetic differences are expected to remain stable under varied environmental conditions. Furthermore, high estimates of heritability indicated that these traits could be used readily in breeding for light interception efficiency in potato. A trait can respond to selection only when it has heritable genetic variation (Falconer and Mackay, 1996).

### 3.8. *Genetic mapping*

Among a total of 566 markers, 325 segregated due to polymorphism in the maternal (SH) parent <ab × aa>, while 241 segregated from the paternal (RH) parent <aa × ab>. Out of 566 markers, a total of 407 markers were mapped and the total data set was split into maternal (SH) and paternal (RH) data sets. Lack of sufficient bridging markers prevented making an integrated map.

The maternal data set could be split into 12 linkage groups at a recombination frequency threshold of 0.25. Twelve parent specific linkage groups were obtained for both SH and RH (Figs. 2.8-2.9). However, linkage group I was divided into two subgroups (denoted as IA and IB, respectively) in the paternal (RH) map due to a lack of a sufficient number of in-between markers. Ninety-five of the 325 AFLP SH markers could not be assigned to the SH linkage groups. In case of RH markers, 64 out of 241 markers could not be assigned to the RH linkage groups. The number of AFLP markers finally retained in the maternal and paternal maps was therefore 230 and 177, respectively, covering the genome size of 1902.9 cM.

The length of the linkage groups in SH parental map ranged from 35.7 cM to 129.3 cM with a median distance of 2.0 cM between the loci. The RH parental map ranged from 28.0 to 101.1 cM and the median distance between loci was 2.5 cM. In both parental maps, the largest gap between loci was on linkage group X of 10.5 cM and 14.1 cM in SH and RH, respectively.

Our linkage map was generally consistent with the ultra-dense map described by Van Os et al. (2006). However, the SH linkage groups VIII and X were 37% and RH linkage group VII was 29% shorter than in the ultra-dense map of Van Os et al. (2006). This discrepancy may simple be due to differences in the size of SH × RH mapping populations (cf. Materials and Methods).

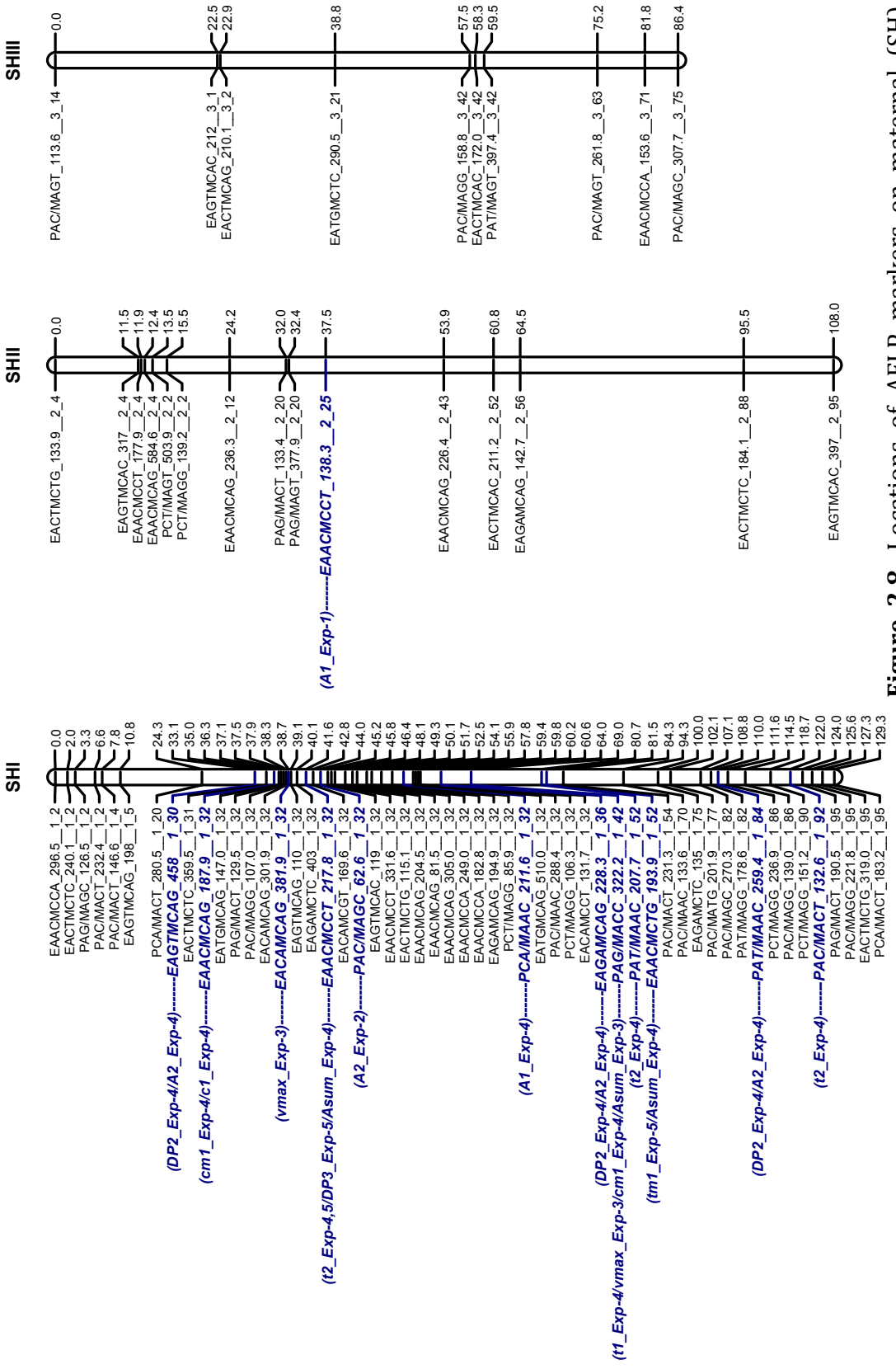


**Figure 2.8.** Locations of AFLP markers on maternal (SH) map (linkage groups I-III). The number on *right side* is the genetic distance in centiMorgans (cM), *left side* is marker designations. The marker in bold shows the position of QTL associated with traits, across environments.

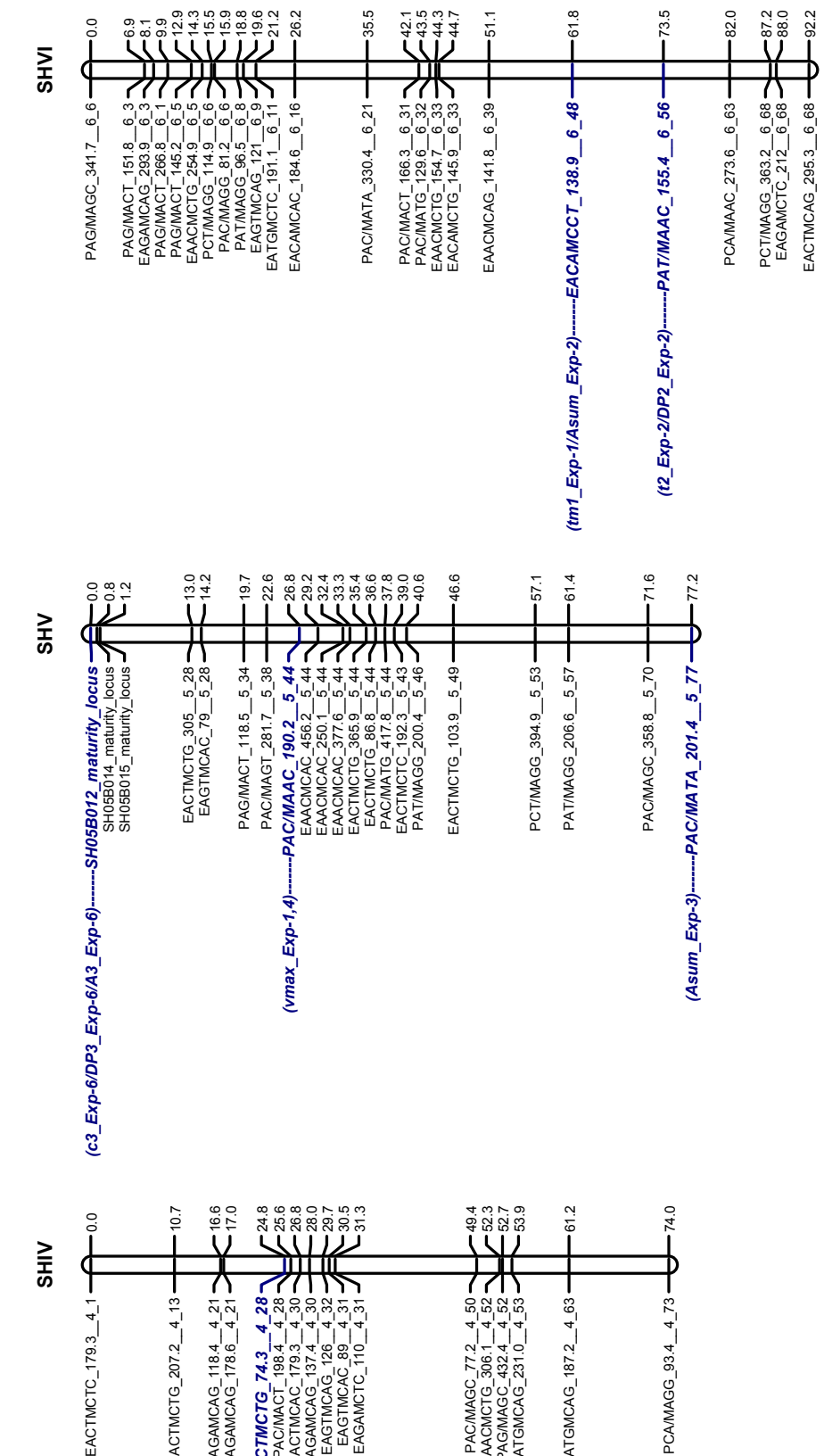


**Figure 2.8**. (*continued*) Locations of AFLP markers on maternal (SH) map (linkage groups IV-VI). The number on *right side* is the genetic distance in centiMorgans (cM), *left side* is marker designations. The marker in bold shows the position of QTL associated with traits, across environments.

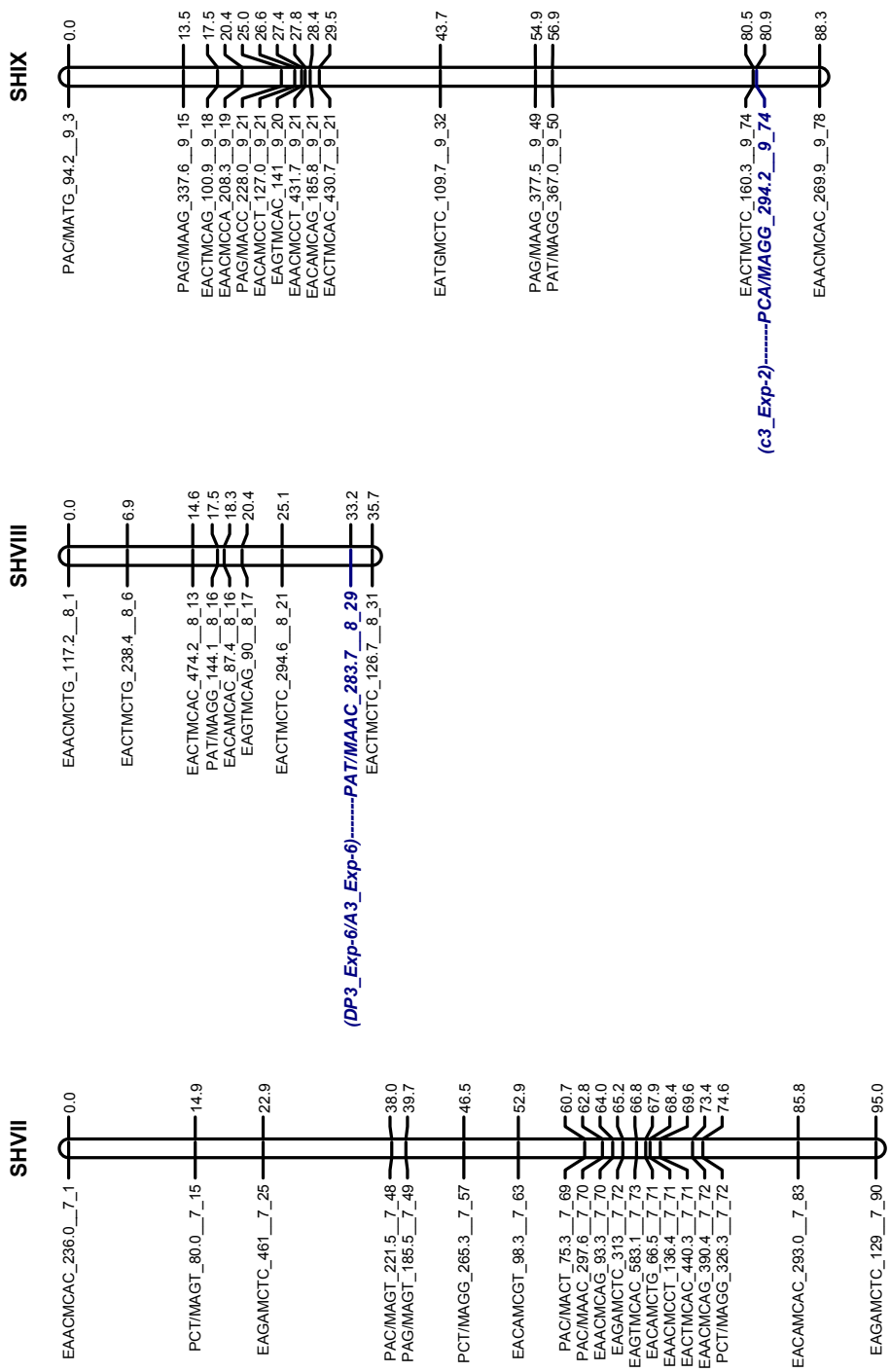


**Figure 2.8.** (*continued*) Locations of AFLP markers on maternal (SH) map (linkage groups VII-IX). The number on *right side* is the genetic distance in centiMorgans (cM), *left side* is marker designations. The marker in bold shows the position of QTL associated with traits, across environments.

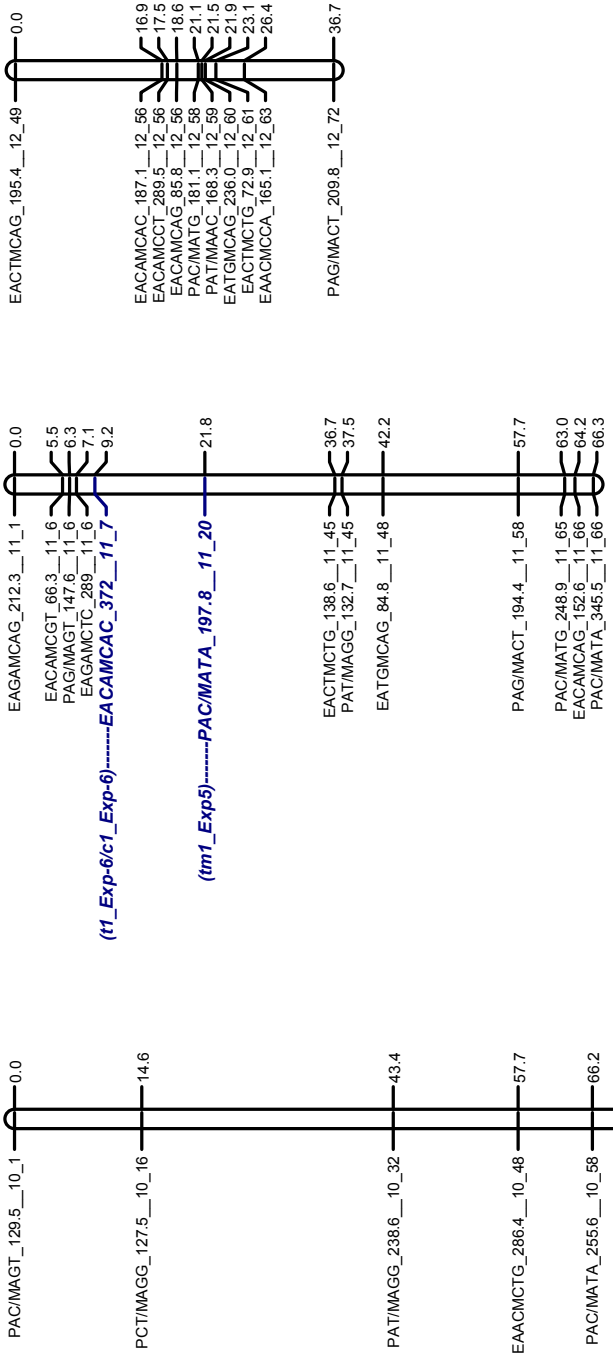


**Figure 2.8.** (*continued*) Locations of AFLP markers on maternal (SH) map (linkage groups X-XII). The number on *right side* is the genetic distance in centiMorgans (cM), *left side* is marker designations. The marker in bold shows the position of QTL associated with traits, across environments.

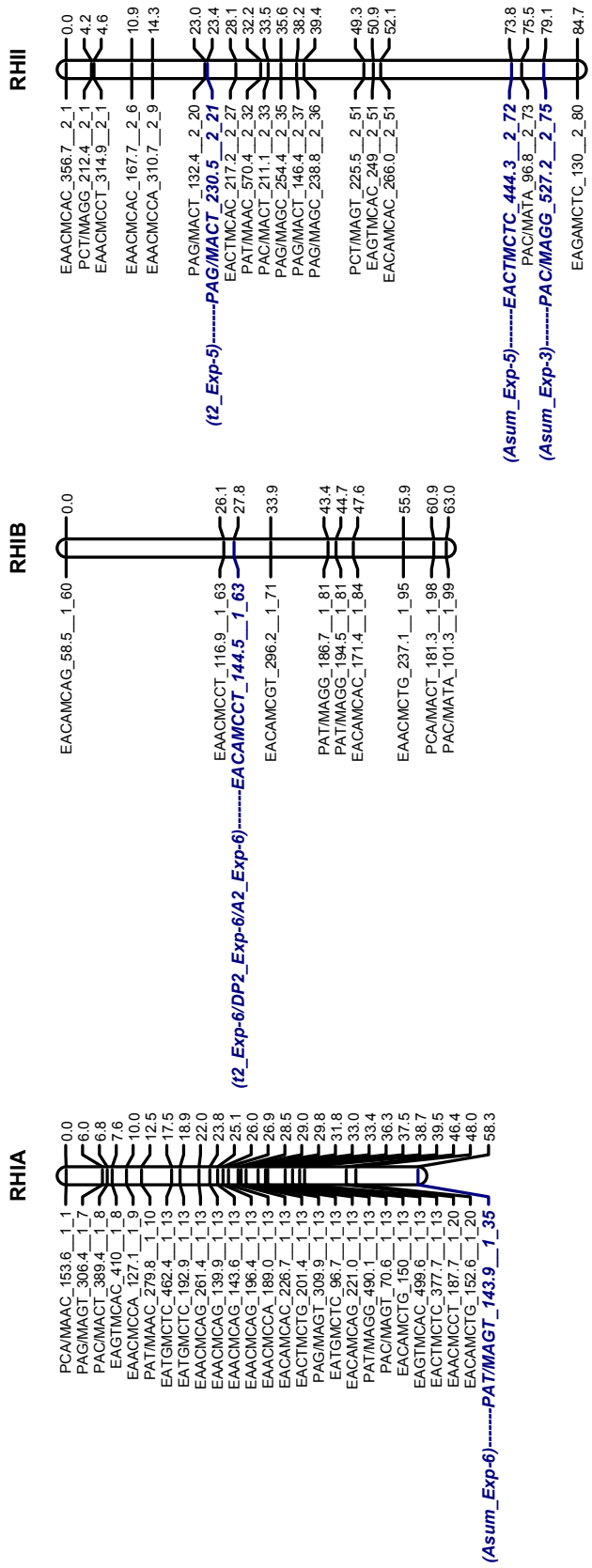


**Figure 2.9.** Locations of AFLP markers on paternal (RH) map (linkage groups I-II). The number on *right side* is the genetic distance in centiMorgans (cM), *left side* is marker designations. The marker in bold shows the position of QTL associated with traits, across environments.

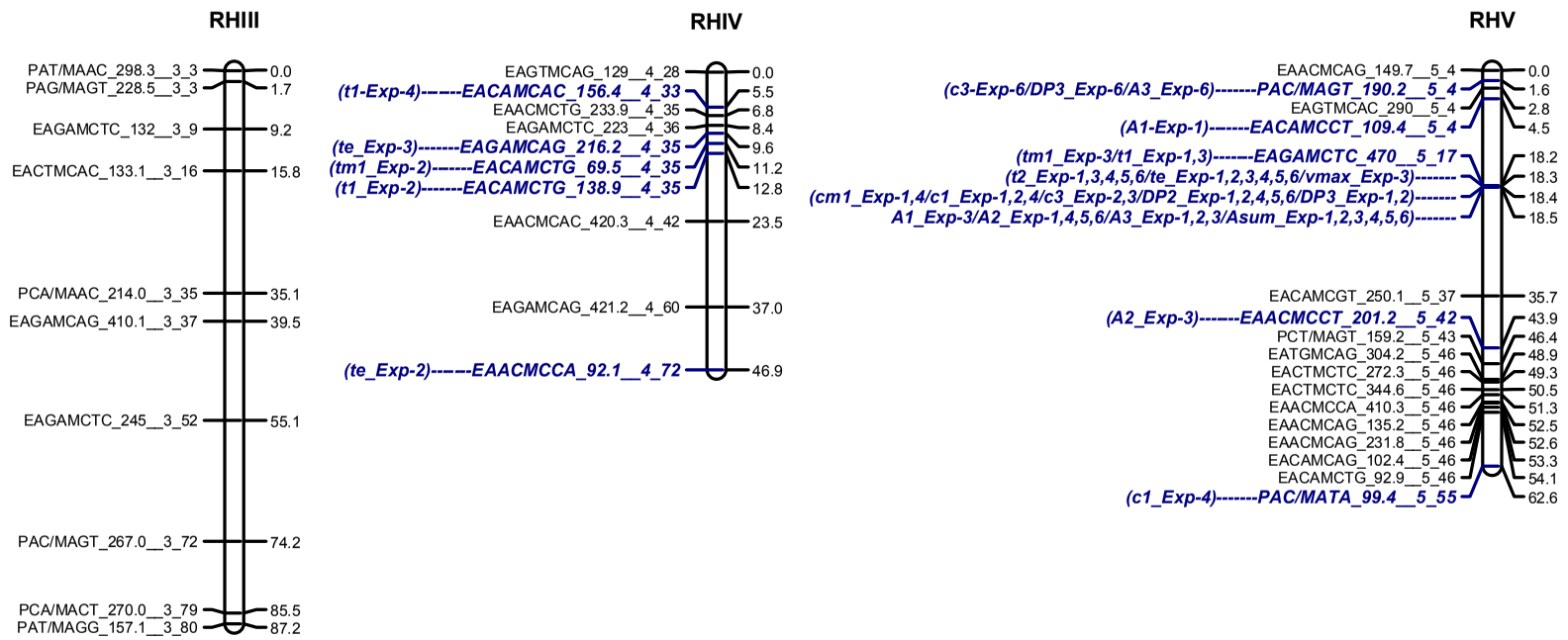


**Figure 2.9.** (*continued*) Locations of AFLP markers on paternal (RH) map (linkage groups III-V). The number on *right side* is the genetic distance in centiMorgans (cM), *left side* is marker designations. The marker in bold shows the position of QTL associated with traits, across environments.

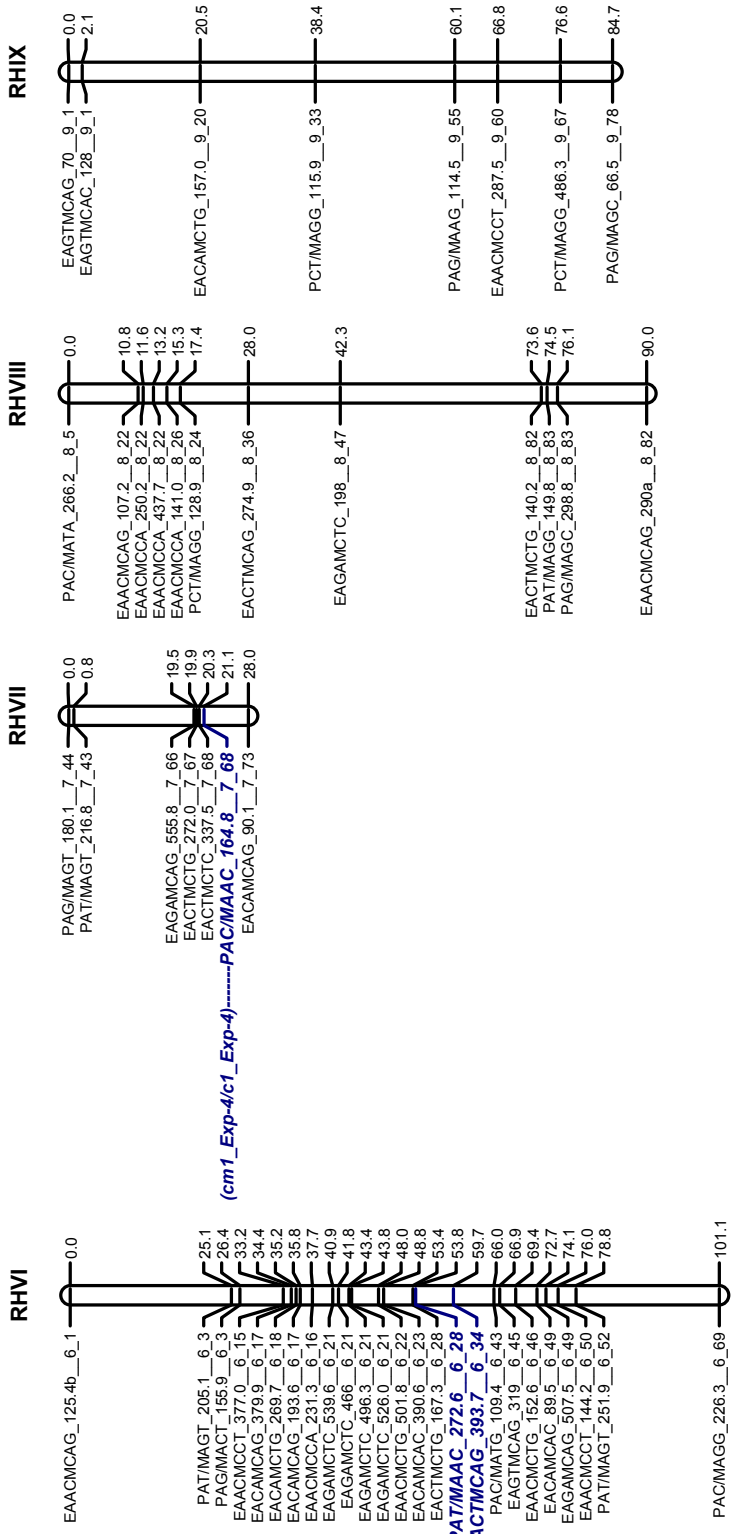


**Figure 2.9.** (*continued*) Locations of AFLP markers on paternal (RH) map (linkage groups VI-IX). The number on *right side* is the genetic distance in centiMorgans (cM), *left side* is marker designations. The marker in bold shows the position of QTL associated with traits, across environments.

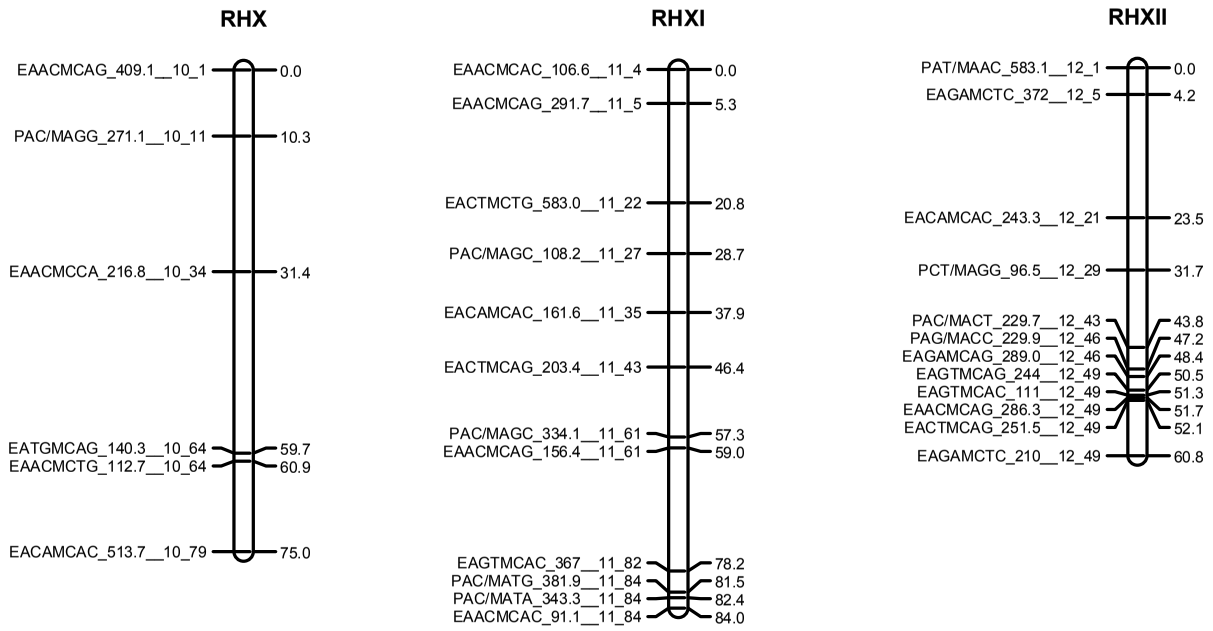


**Figure 2.9.** (*continued*) Locations of AFLP markers on paternal (RH) map (linkage groups X-XII). The number on *right side* is the genetic distance in centiMorgans (cM), *left side* is marker designations. The marker in bold shows the position of QTL associated with traits, across environments.

### 3.9. *QTL detection*

QTL analysis for the five model parameters and nine derived traits was conducted separately for the six environments (i.e. experiments). In total 41 QTLs were identified on both SH and RH parental genomes across all six environments (Figs. 2.8-2.9). In the SH genome, 23 QTLs were associated with eight linkage groups (I, II, IV, V, VI, VIII, IX, and XI). Eighteen QTLs were shared by the RH genome on six linkage groups (I, II, IV, V, VI, and VII). The numbers of QTLs detected for each parental chromosome are listed in (Table 2.7).

Table 2.8 summarises the list of QTLs detected, their parental chromosomes and map positions and their characteristics (i.e. additive effects and variance explained ($R^2$) for each of the trait investigated for individual environment). All the QTLs detected were significant at ($P$<0.05) with $-\log_{10}(P)$ values ranging from 3.47 to 52.33. The total fraction of phenotypic variance explained by effects of each QTL were moderate (ranging from <0.1% to 74%), but a high percentage of phenotypic variance was accounted for when considering the global $R^2$ (ranging from 28% to 82%) (Table 2.8).

Detailed investigation of the QTLs identified for five model parameters showed that five QTLs were detected for $t_{m1}$ scattered across linkage groups (SH I, SH VI, SH XI, RH IV, and RH V) in all the experiments except Exps 4 and 6, where no QTL was found (Table 2.8). The fraction of phenotypic variance explained by individual QTLs ranged from 12% to 16%. The QTL (116_5_17) detected in Exp 3 shared the maximum negative additive effect (-4.1 *td*) and explained the maximum (16%) phenotypic variance. However, two QTLs detected in Exp 5 (i.e. 66_1_52 and

**Table 2.7.** Distribution of QTLs detected on parental genomes.

| SH | | RH | |
|---|---|---|---|
| Linkage group | No. of QTLs | Linkage group | No. of QTLs |
| I | 12 | IA | 1 |
| II | 1 | IB | 1 |
| IV | 1 | II | 3 |
| V | 3 | IV | 5 |
| VI | 2 | V | 5 |
| VIII | 1 | VI | 2 |
| IX | 1 | VII | 1 |
| XI | 2 | | |
| Total | 23 | | 18 |

**Table 2.8.** Main characteristics of quantitative trait loci (QTL) identified for five model parameters ($t_{m1}$, $t_1$, $t_2$, $t_e$, $v_{max}$) and nine derived secondary traits ($c_{m1}$, $c_1$, $c_3$, $D_{P2}$, $D_{P3}$, $A_1$, $A_2$, $A_3$, $A_{sum}$) within the 'SH × RH' population per individual experiment (i.e. environment.). Data given in table are from the CIM mapping method. QTLs marked as bold are detected only by the CIM method, otherwise by both the CIM and SIM methods. Exp., experiment; position, position of maximum $-\log_{10}(P)$; a, additive effect of the presence of parental allele at a marker; $R^2$, the individual contribution of one QTL to the variation in a trait; global $R^2$, the fraction of the total variation explained by QTLs of the same trait within single environment ; *td*, thermal day. Symbol '–' means no QTL was detected.

| Parameter | Exp. | QTL | Linkage group | Marker name | Position (cM) | $-\log_{10}(P)$ | a | $R^2$ | Global $R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| $t_{m1}$ (*td*) | 1 | 199_6_48 | SH VI | EACAMCCT_138.9__6_48 | 61.8 | 3.47 | 2.902 | 0.13 | |
| | 2 | 99_4_35 | RH IV | EACAMCTG_69.5__4_35 | 11.2 | 3.67 | 1.975 | 0.14 | |
| | 3 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 3.95 | -4.113 | 0.16 | |
| | 4 | – | – | – | – | – | – | – | |
| | 5 | 66_1_52 | SH I | EAACMCTG_193.9__1_52 | 81.5 | 4.61 | 2.427 | 0.16 | 0.29 |
| | | 293_11_20 | SH XI | PAC/MATA_197.8__11_20 | 21.8 | 3.584 | -2.095 | 0.12 | |
| | 6 | – | – | – | – | – | – | – | |
| $t_1$ (*td*) | 1 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 6.23 | 7.404 | 0.23 | |
| | 2 | 98_4_35 | RH IV | EACAMCTG_138.9__4_35 | 12.8 | 3.48 | 3.167 | 0.13 | |
| | 3 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 18.02 | -26.586 | 0.60 | |
| | 4 | 63_1_42 | SH I | PAG/MACC_322.2__1_42 | 69 | 4.738 | -5.754 | 0.17 | 0.28 |
| | | **96_4_33** | **RH IV** | **EACAMCAC_156.4__4_33** | **5.5** | 3.423 | 4.691 | 0.11 | |
| | 5 | – | – | – | – | – | – | – | |
| | 6 | 291_11_7 | SH XI | EACAMCAC_372__11_7 | 9.2 | 3.371 | -2.591 | 0.14 | |

**Table 2.8.** (Continued)

| Parameter | Exp. | QTL | Linkage group | Marker name | Position (cM) | -log$_{10}$($P$) | a | $R^2$ | Global $R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| $t_2$ ($td$) | 1 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 6.66 | -9.584 | 0.24 | |
| | 2 | 200_6_56 | SH VI | PAT/MAAC_155.4__6_56 | 73.5 | 3.8 | 8.055 | 0.15 | |
| | 3 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 19.52 | -31.694 | 0.49 | 0.56 |
| | | **154_6_34** | **RH VI** | **EACTMCAG_393.7__6_34** | **59.7** | 3.53 | 10.453 | 0.04 | |
| | 4 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 17.24 | -26.021 | 0.55 | 0.67 |
| | | **39_1_32** | **SH I** | **EAACMCCT_217.8__1_32** | **41.6** | 1.445 | 6.521 | 0.10 | |
| | | **67_1_52** | **SH I** | **PAT/MAAC_207.7__1_52** | **80.7** | 0.248 | 1.915 | 0.01 | |
| | | **81_1_92** | **SH I** | **PAC/MACT_132.6__1_92** | **122** | 1.555 | 5.433 | 0.01 | |
| | 5 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 16.008 | -27.999 | 0.52 | 0.64 |
| | | 39_1_32 | SH I | EAACMCCT_217.8__1_32 | 41.6 | 3.096 | 9.011 | 0.14 | |
| | | **64_2_21** | **RH II** | **PAG/MACT_230.5__2_21** | **23.4** | 1.913 | -6.698 | 0.01 | |
| | 6 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 10.018 | -18.544 | 0.27 | 0.43 |
| | | **47_1_63** | **RH IB** | **EACAMCCT_144.5__1_63** | **27.8** | 5.463 | 11.577 | 0.08 | |

**Table 2.8.** (Continued)

| Parameter | Exp. | QTL | Linkage group | Marker name | Position (cM) | -log$_{10}$($P$) | a | $R^2$ | Global $R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| $t_e$ ($td$) | 1 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 19.5 | -19.351 | 0.51 | |
| | 2 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 24.25 | -27.232 | 0.55 | 0.62 |
| | | **108_4_72** | **RH IV** | **EAACMCCA_92.1__4_72** | **46.9** | 3.93 | 8.408 | 0.02 | |
| | 3 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 26.91 | -29.497 | 0.58 | 0.68 |
| | | **101_4_35** | **RH IV** | **EAGAMCAG_216.2__4_35** | **9.6** | 3.95 | 7.58 | 0.03 | |
| | | **153_6_28** | **RH VI** | **PAT/MAAC_272.6__6_28** | **53.8** | 3.62 | 7.112 | 0.02 | |
| | 4 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 20.612 | -32.356 | 0.65 | |
| | 5 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 19.527 | -24.133 | 0.63 | |
| | 6 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 52.33 | -49.912 | 0.74 | |
| $v_{max}$ (%) | 1 | 170_5_44 | SH V | PAC/MAAC_190.2__5_44 | 26.8 | 5.66 | 22.66 | 0.21 | |
| | 2 | – | – | – | – | – | – | – | |
| | 3 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 26.28 | -54.862 | 0.56 | 0.65 |
| | | **21_1_32** | **SH I** | **EACAMCAG_381.9__1_32** | **38.7** | 3.8 | 4.243 | 0.02 | |
| | | **63_1_42** | **SH I** | **PAG/MACC_322.2__1_42** | **69** | 4.78 | 16.533 | 0.12 | |
| | 4 | 170_5_44 | SH V | PAC/MAAC_190.2__5_44 | 26.8 | 4.291 | 8.836 | 0.18 | |
| | 5 | – | – | – | – | – | – | – | |
| | 6 | – | – | – | – | – | – | – | |

**Table 2.8.** (Continued)

| Parameter | Exp. | QTL | Linkage group | Marker name | Position (cM) | -log$_{10}$($P$) | a | $R^2$ | Global $R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| $c_{m1}$ (% $td^{-1}$) | 1 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 7.8 | -2.413 | 0.28 | |
| | 2 | – | – | – | – | – | – | – | |
| | 3 | – | – | – | – | – | – | – | |
| | 4 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 5.21 | -3.987 | 0.16 | 0.41 |
| | | 18_1_32 | SH I | EAACMCAG_187.9__1_32 | 36.3 | 4.23 | 1.272 | 0.06 | |
| | | 63_1_42 | SH I | PAG/MACC_322.2__1_42 | 69 | 4.27 | 2.381 | 0.12 | |
| | | **173_7_68** | **RH VII** | **PAC/MAAC_164.8__7_68** | **21.1** | 3.55 | 2.997 | 0.08 | |
| | 5 | – | – | – | – | – | – | – | |
| | 6 | – | – | – | – | – | – | – | |
| $c_1$ (% $td^{-1}$) | 1 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 7.34 | -1.165 | 0.26 | |
| | 2 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 3.63 | -0.693 | 0.14 | |
| | 3 | – | – | – | – | – | – | – | |
| | 4 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 3.88 | -1.055 | 0.13 | 0.44 |
| | | 18_1_32 | SH I | EAACMCAG_187.9__1_32 | 36.3 | 5.82 | 1.236 | 0.18 | |
| | | **131_5_55** | **RH V** | **PAC/MATA_99.4__5_55** | **62.6** | 3.49 | -0.387 | 0.03 | |
| | | 173_7_68 | RH VII | PAC/MAAC_164.8__7_68 | 21.1 | 3.80 | 1.081 | 0.11 | |
| | 5 | – | – | – | – | – | – | – | |
| | 6 | 291_11_7 | SH XI | EACAMCAC_372__11_7 | 9.2 | 3.477 | 0.899 | 0.14 | |

**Table 2.8.** (Continued)

| Parameter | Exp. | QTL | Linkage group | Marker name | Position (cM) | -log$_{10}$($P$) | a | $R^2$ | Global $R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| $c_3$ (% $td^{-1}$) | 1 | – | – | – | – | – | – | – | |
| | 2 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 8.76 | 4.649 | 0.29 | 0.39 |
| | | **265_9_74** | **SH IX** | **PCA/MAGG_294.2__9_74** | **80.9** | 3.64 | 2.619 | 0.13 | |
| | 3 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 6.905 | -5.338 | 0.28 | |
| | 4 | – | – | – | – | – | – | – | |
| | 5 | – | – | – | – | – | – | – | |
| | 6 | **1_5_12** | **SH V** | **SH05B012_maturity_locus** | **0** | 3.28 | 3.595 | 0.07 | 0.28 |
| | | 115_5_4 | RH V | PAC/MAGT_190.2__5_4 | 1.6 | 5.641 | 4.523 | 0.18 | |
| $D_{P2}$ ($td$) | 1 | 116_5_17 | RHV | EAGAMCTC_470__5_17 | 18.2 | 11.48 | -16.987 | 0.37 | |
| | 2 | **133_4_28** | **SH IV** | **EACTMCTG_74.3__4_28** | **24.8** | 4.09 | 6.655 | 0.09 | 0.35 |
| | | 200_6_56 | SH VI | PAT/MAAC_155.4__6_56 | 73.5 | 4.30 | 6.996 | 0.13 | |
| | | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 4.08 | -10.208 | 0.14 | |
| | 3 | – | – | – | – | – | – | – | |
| | 4 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 26.28 | -30.089 | 0.56 | 0.70 |
| | | **14_1_30** | **SH I** | **EAGTMCAG_458__1_30** | **33.1** | 6.82 | 2.83 | 0.03 | |
| | | **62_1_36** | **SH I** | **EAGAMCAG_228.3__1_36** | **64** | 8.39 | 9.433 | 0.15 | |
| | | **76_1_84** | **SH I** | **PAT/MAAC_259.4__1_84** | **110** | 4.15 | 4.61 | 0.02 | |
| | 5 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 11.983 | -31.322 | 0.45 | |
| | 6 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 8.355 | -17.625 | 0.22 | 0.38 |
| | | **47_1_63** | **RH IB** | **EACAMCCT_144.5__1_63** | **27.8** | 4.686 | 11.283 | 0.04 | |

**Table 2.8.** (Continued)

| Parameter | Exp. | QTL | Linkage group | Marker name | Position (cM) | -log$_{10}$($P$) | a | $R^2$ | Global $R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| $D_{P3}$ ($td$) | 1 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 5.26 | -9.768 | 0.20 | |
| | 2 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 14.39 | -19.569 | 0.42 | |
| | 3 | – | – | – | – | – | – | – | |
| | 4 | – | – | – | – | – | – | – | |
| | 5 | 39_1_32 | SH I | EAACMCCT_217.8__1_32 | 41.6 | 4.101 | -8.657 | 0.17 | |
| | 6 | **1_5_12** | **SH V** | **SH05B012_maturity_locus** | **0** | 4.573 | -8.988 | 0.08 | 0.46 |
| | | **242_8_29** | **SH VIII** | **PAT/MAAC_283.7__8_29** | **33.2** | 4.134 | -6.785 | 0.08 | |
| | | 115_5_4 | RH V | PAC/MAGT_190.2__5_4 | 1.6 | 9.326 | -12.803 | 0.24 | |
| $A_1$ ($td$ %) | 1 | 102_2_25 | SH II | EAACMCCT_138.3__2_25 | 37.5 | 3.48 | 275.871 | 0.13 | 0.33 |
| | | 114_5_4 | RH V | EACAMCCT_109.4__5_4 | 4.5 | 6.23 | 412.691 | 0.22 | |
| | 2 | – | – | – | – | – | – | – | |
| | 3 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 20.042 | -2246.416 | 0.64 | |
| | 4 | 58_1_32 | SH I | PCA/MAAC_211.6__1_32 | 57.8 | 4.77 | -458.085 | 0.18 | |
| | 5 | – | – | – | – | – | – | – | |
| | 6 | – | – | – | – | – | – | – | |

**Table 2.8.** (Continued)

| Parameter | Exp. | QTL | Linkage group | Marker name | Position (cM) | -log$_{10}$($P$) | a | $R^2$ | Global $R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| $A_2$ ($td$ %) | 1 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 12.35 | -1764.776 | 0.39 | |
| | 2 | 53_1_32 | SH I | PAC/MAGC_62.6__1_32 | 44 | 4.5 | 987.678 | 0.17 | |
| | 3 | 118_5_42 | RH V | EAACMCCT_201.2__5_42 | 43.9 | 4.398 | -1215.599 | 0.18 | |
| | 4 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 25.9 | -3039.945 | 0.55 | 0.70 |
| | | **62_1_36** | **SH I** | **EAGAMCAG_228.3__1_36** | **64** | 8.48 | 973.111 | 0.15 | |
| | | **76_1_84** | **SH I** | **PAT/MAAC_259.4__1_84** | **110** | 4.17 | 469.087 | 0.02 | |
| | | **14_1_30** | **SH I** | **EAGTMCAG_458__1_30** | **33.1** | 6.86 | 281.737 | 0.03 | |
| | 5 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 16.32 | -3198.355 | 0.45 | |
| | 6 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 8.35 | -1768.77 | 0.24 | 0.37 |
| | | **47_1_63** | **RH IB** | **EACAMCCT_144.5__1_63** | **27.8** | 4.634 | 1124.769 | 0.07 | |
| $A_3$ ($td$ %) | 1 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 7.32 | -771.481 | 0.26 | |
| | 2 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 14.76 | -1251.073 | 0.43 | |
| | 3 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 4.473 | -787.222 | 0.18 | |
| | 4 | – | – | – | – | – | – | – | |
| | 5 | 39_1_32 | SH I | EAACMCCT_217.8__1_32 | 41.6 | 3.68 | -436.12 | 0.14 | |
| | 6 | **1_5_12** | **SH V** | **SH05B012_maturity_locus** | **0** | 4.37 | -559.686 | 0.08 | 0.46 |
| | | **242_8_29** | **SH VIII** | **PAT/MAAC_283.7__8_29** | **33.2** | 3.85 | -422.482 | 0.08 | |
| | | 115_5_4 | RH V | PAC/MAGT_190.2__5_4 | 1.6 | 6.72 | -804.803 | 0.24 | |

**Table 2.8.** (Continued)

| Parameter | Exp. | QTL | Linkage group | Marker name | Position (cM) | -log$_{10}$($P$) | a | $R^2$ | Global $R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| $A_{sum}$ ($td$ %) | 1 | 116_5_17 | RH V | EAGAMCTC_470_5_17 | 18.2 | 19.65 | -2359.408 | 0.50 | 0.57 |
| | | 43_1_35 | RH IA | PAT/MAGT_143.9_1_35 | 58.3 | 3.6 | 786.981 | <0.1 | |
| | 2 | 116_5_17 | RH V | EAGAMCTC_470_5_17 | 18.2 | 21.09 | -2188.154 | 0.52 | 0.59 |
| | | **199_6_48** | **SH VI** | **EACAMCCT_138.9_6_48** | **61.8** | 3.91 | 719.654 | 0.03 | |
| | 3 | 116_5_17 | RH V | EAGAMCTC_470_5_17 | 18.2 | 28.68 | -4112.081 | 0.69 | 0.82 |
| | | **63_1_42** | **SH I** | **PAG/MACC_322.2_1_42** | **69** | 3.953 | 878.855 | 0.07 | |
| | | **179_5_77** | **SH V** | **PAC/MATA_201.4_5_77** | **77.2** | 4.883 | 974.202 | <0.1 | |
| | | **81_2_75** | **RH II** | **PAC/MAGG_527.2_2_75** | **79.1** | 4.481 | -938.074 | <0.1 | |
| | 4 | 116_5_17 | RH V | EAGAMCTC_470_5_17 | 18.2 | 40.06 | -2996.801 | 0.67 | 0.73 |
| | | **66_1_52** | **SH I** | **EAACMCTG_193.9_1_52** | **81.5** | 4.11 | 419.656 | 0.06 | |
| | | **39_1_32** | **SH I** | **EAACMCCT_217.8_1_32** | **41.6** | 4.51 | 552.856 | 0.08 | |
| | 5 | 116_5_17 | RH V | EAGAMCTC_470_5_17 | 18.2 | 29.21 | -2991.844 | 0.59 | 0.65 |
| | | **79_2_72** | **RH II** | **EACTMCTC_444.3_2_72** | **73.8** | 3.7 | -815.825 | <0.1 | |
| | 6 | 116_5_17 | RH V | EAGAMCTC_470_5_17 | 18.2 | 18.77 | -2185.245 | 0.49 | |

293_11_20) together explained 29% of the phenotypic variance with their additive effects ranging from (2.4 *td* to -2.1 *td*).

Six QTLs were associated with $t_1$ on linkage groups (SH I, SH XI, RH IV, and RH V) across environments with their additive effects ranging from (-2.9 *td* to -26.6 *td*) with phenotypic variance explained by individual QTL ranging from (11% to 60%) (Table 2.8). Majority of environments showed one QTL except Exp 4, where two QTLs were found with 28% combined explained phenotypic variance. No QTL could be found in Exp 5. Among the QTLs detected, the QTL (116_5_17) on linkage group RH V was a major one with maximum additive effect of (-26.6 *td*). This QTL was detected in both Exps 1 and 3 explaining 23% and 60 % of phenotypic variance, respectively.

A total of eight different QTLs were detected for $t_2$ across the environments with their additive effects ranging from (1.9 *td* to -31.7 *td*) (Table 2.8). These QTLs were associated with five parental linkage groups (SH I, SH VI, RH IB, RH II, and RH V) explaining the phenotypic variance ranging from (1% to 55%). Two or more QTLs were detected for the majority of environments. The QTL (116_5_17) on linkage group RH V was a major one detected consistently throughout the environments apart from Exp 2. This QTL had a negative additive effect throughout the experiments with maximum effect in Exp 3. The maximum phenotypic variance by this QTL was in Exp 4 (i.e. 55%).

Four QTLs were associated with $t_e$ across the environments explaining the total phenotypic variance ranging from 2% to 74% (Table 2.8). These QTLs were mainly located on three paternal linkage groups (RH IV, RH V, RH VI) with their additive effects ranging from 7.1 *td* to -49.9 *td*. The majority of environments showed one QTL except Exps 2 and 3, where two and three QTLs were found with 62% and 68% combined explained phenotypic variance, respectively. Among the QTLs detected, the QTL (116_5_17) on linkage group RHV was a major one in all the six environments with maximum additive effect of (-49.9 *td*) in Exp 6. Only three additional minor QTLs, one in Exp 2 (108_4_72) and two in Exp 3 (101_4_35 and 153_6_28) were detected, with their additive effects ranging from 7.1 *td* to 8.4 *td* with only 2-3% of associated phenotypic variance.

Four individual QTLs were found for $v_{max}$ located on the three parental linkage groups (SH I, SH V, and RH V) (Table 2.8). Their associated additive effects ranged from 4.2% to -54.9% and the phenotypic variance ranged from 2% to 56%. QTLs were detected in only half of the environments (i.e. Exps 1, 3, and 4). Among these environments, a total of three QTLs were detected in Exp 3 with their 65% combined phenotypic explained variance. The QTL (116_5_17) on linkage group RHV was a major one in this environment with maximum additive effect of (-54.9 %). A QTL (170_5_44) associated with linkage group SH V was commonly detected in both Exps

1 and 4 with a maximum of 22.7 % additive effect and 21% associated phenotypic variance in Exp 1.

For the traits related with canopy growth rate, four QTLs were detected for $c_{m1}$, five QTLs for $c_1$, and four QTLs for $c_3$ (Table 2.8). These QTLs were scattered on six parental linkage groups (SH I, SH V, SH IX, SH XI, RH V, RH VII). The phenotypic variance explained by QTLs ranged from (3% to 29%). In case of $c_{m1}$, one and four QTLs were found in Exps 1 and 4, respectively. No QTLs were found in other environments. The four QTLs found in Exp 4 jointly explained 41% of the phenotypic variance. However, among these QTLs, (116_5_17) on linkage group RH V was a major QTL with the maximum additive effect of -3.9 % $td^{-1}$. This QTL was also common in both environments (Exps 1 and 4) explaining 28% and 16% phenotypic variance for $c_{m1}$. In case of $c_1$, one QTL was detected in Exps 1, 2, and 6, whereas four QTLs could be found in Exp 4. No QTLs were found in Exps 3 and 5. The three QTLs found in Exp 4 jointly explained 44% of the phenotypic variance. The major QTL (116_5_17) on linkage group RH V was commonly found in Exps 1, 2, and 4 with the additive effect ranging from -0.7 to -1.17 % $td^{-1}$ and 13% to 26% explained phenotypic variance. In total four QTLs were detected for $c_3$, two each in Exps 2 and 6, one in Exp 3, whereas no QTLs were found in the other environments. The combined phenotypic variance in Exps 2 and 6 was 39% and 28%, respectively. The major QTL (116_5_17) located on linkage group RH V was commonly detected in Exps 2 and 3 with positive (4.6 % $td^{-1}$) and negative (-5.3 % $td^{-1}$) additive effects with 29% and 28% explained phenotypic variance, respectively (Table 2.8). This switch from positive to negative effect is very interesting phenomenon and might be related with the uniqueness of these two environments as Exp 3 was clearly lower in N availability than Exp 2 (Table 2.1). Growth rate can be seen as the integration of a wide range of processes and thus may depend on many factors. As we already mentioned in previous sections, the canopy senescence rate was slowed down to such an extent that the end of crop cycle ($t_e$) occurred very late in the said environment (Table 2.2).

For the traits related with total duration of canopy maximum and decline phases (i.e. $D_{P2}$ and $D_{P3}$), six and five QTLs for each were detected, respectively across the environments (Table 2.8). These QTLs were scattered on seven parental linkage groups (SH I, SH IV, SH V, SH VI, SH VIII, RH IB, and RH V). The phenotypic variance explained by QTLs ranged from 2% to 56%. For $D_{P2}$, one QTL was detected in Exps 2 and 5, while three, four and two QTLs were detected in Exps 2, 4, and 6, respectively. No QTL could be detected in Exp 3. The four QTLs found in Exp 4 jointly explained 70% of the phenotypic variance. Among the total QTLs detected for this trait, 116_5_17 on linkage group RHV was a major QTL detected in nearly all environments with its additive effects ranging from -10.2 *td* to -31.3 *td* and explaining 14% to 56%

phenotypic variance for $D_{P2}$. In case of $D_{P3}$, one QTL was detected in Exps 1, 2, and 5, whereas three QTLs were found in Exp 6. No QTLs were found in Exps 3 and 4. The three QTLs found in Exp 6 jointly explained 46% of the phenotypic variance. The major QTL was 116_5_17 on linkage group RHV commonly found in Exps 1 and 2 with the additive effect ranging from -9.8 *td* to -19.6 *td* and 20% to 42% explained phenotypic variance, respectively.

For the traits related with the area under the canopy growth curve (i.e. $A_1$, $A_2$, $A_3$, and $A_{sum}$), QTLs detected were scattered on nine parental linkage groups (SH I, SH II, SH V, SH VI, SH VIII, RH IA, RH IB, RH II, and RH V) (Table 2.8). The phenotypic variance explained by QTLs ranged from <0.1% to 69%. A total four QTLs were detected for $A_1$, i.e. two in Exp 1 and one each in Exps 3 and 4, whereas no QTLs were found in the other environments. The phenotypic variance explained by QTLs ranged from 13% to 64%. The combined phenotypic variance for two QTLs in Exp 1 was 33%. Among the QTLs detected 116_5_17 located on linkage group RHV was considered a major QTL with its associated additive effect of -2246.4 *td* % and with 64% phenotypic variance in Exp 3. Seven QTLs were found for $A_2$ throughout environments with their explained variance ranging from 2% to 55%. Among the environments, one QTL was detected in Exps 1, 2, 3, and 5, whereas four and two QTLs were estimated in Exps 4 and 6, respectively. The combined phenotypic variance accounted by QTLs in Exps 4 and 6 was 70% and 37%, respectively. The major QTL (116_5_17) on linkage group RH V was commonly found in Exps 1, 4, 5, and 6 with the additive effect ranging from -1215.6 *td* % to -3198.4 *td* % and 18% to 55% explained phenotypic variance. In total five QTLs were detected for $A_3$ with phenotypic variance ranging from 8% to 43%. One QTL was found each in Exps 1, 2, 3 and 5; three in Exp 6, whereas no QTLs were found in Exp 4. The combined QTLs explained phenotypic variance in Exp 6 was 46%. QTL 116_5_17 located on linkage group RHV was a major one and commonly detected in Exps 1, 2, and 3 with additive effects ranging from -771.5 *td* % to -1251.1 *td* % with 18% to 43% range of phenotypic explained variance. In case of $A_{sum}$, we estimated the maximum of nine QTLs across the environments. The phenotypic variance explained by individual QTLs ranged from <1% to 69%. The number of QTLs found in the various environments was: one QTL in Exp 6, two in Exps 1, 2, and 5, three in Exp 4, and four QTLs in Exp 3 were found (Table 2.8). The combined phenotypic variance explained by the QTLs ranged from 57% to 82%. The QTL 116_5_17 on linkage group RH V was detected in all the environments explaining the range of 49% to 69% phenotypic variance for $A_{sum}$. This QTL was associated with a major additive effect of -4112.1 *td* % in Exp 3.

In summary, QTLs with major effects were associated with paternal (RH) linkage groups, especially RH V (Table 2.9), where in total of five QTLs were detected

(Table 2.7). QTLs on this linkage group had negative additive effects, indicating that RH alleles on this linkage group share an antagonistic effect on the physiological traits related with canopy cover. One particular QTL (116_5_17) on this linkage group was detected for nearly all traits with a major additive effect and explained most of the total phenotypic variance. Large number of additional QTLs with minor effects was mostly associated with maternal (SH) linkage groups (Tables 2.8 and 2.9). Our results are in line with those by Van den Berg et al. (1996), who also reported that most of the loci had small effects, but a QTL with main effect was found on chromosome V. We also observed the co-localisation of QTLs for many traits. For instance clustering of many QTLs were found on position 18.2 cM on paternal (RH) linkage group (Table 2.10). Here most of the traits (e.g. $t_2$, $D_{P2}$, $A_2$, $A_{sum}$) were tightly linked with QTL (116_5_17) in most of the environments. This could mean that this QTL is playing a pleiotropic role in determining these traits. The phenomenon of pleiotropy can have important implications for our understanding of the nature of genetic correlations between different traits in certain regions of a genome and also for practical applications in breeding because one of the major goals in breeding is to break unfavourable linkage (Jiang and Zeng, 1995). High genetic correlations between these traits confirm these relations (Table 2.5).

**Table 2.9.** List of parental linkage groups with major and additional minor QTLs.

| Parameter | SH linkage group | RH linkage group | |
|---|---|---|---|
| | Minor QTLs | Major QTLs | Minor QTLs |
| $t_{m1}$ | I, VI, XI | V | IV |
| $t_1$ | I, XI | V | IV |
| $t_2$ | I, VI | V | IB, II, VI |
| $t_e$ | – | V | IV, VI |
| $v_{max}$ | I, V | V | – |
| $c_{m1}$ | I | V | VII |
| $c_1$ | I, XI | V | VII |
| $c_3$ | V, IX | V | – |
| $D_{P2}$ | I, IV, VI | V | IB |
| $D_{P3}$ | I, V, VIII | V | – |
| $A_1$ | I, II | V | – |
| $A_2$ | I | V | IB |
| $A_3$ | I, V, VIII | V | – |
| $A_{sum}$ | I, V, VI | V | IA, II |

**Table 2.10.** List of co-localised QTLs i.e. QTLs were same for more than one trait.

| QTL | Linkage group | Marker name | Position (cM) | Exp. 1 | Exp. 2 | Exp. 3 | Exp. 4 | Exp. 5 | Exp. 6 |
|---|---|---|---|---|---|---|---|---|---|
| 14_1_30 | SH I | EAGTMCAG_458__1_30 | 33.1 | | | | $D_{P2}$, $A_2$ | | |
| 18_1_32 | SH I | EAACMCAG_187.9__1_32 | 36.3 | | | | $c_{m1}$,$c_1$ | | |
| 39_1_32 | SH I | EAACMCCT_217.8__1_32 | 41.6 | | | $t_2$, $A_{sum}$ | | $t_2$, $D_{P3}$ | |
| 62_1_36 | SH I | EAGAMCAG_228.3__1_36 | 63.9 | | | | $D_{P2}$, $A_2$ | | |
| 63_1_42 | SH I | PAG/MACC_322.2__1_42 | 68.9 | | | $v_{max}$, $A_{sum}$ | $t_1$, $c_{m1}$ | | |
| 66_1_52 | SH I | EAACMCTG_193.9__1_52 | 81.5 | | | | $A_{sum}$ | $t_{m1}$ | |
| 76_1_84 | SH I | PAT/MAAC_259.4__1_84 | 109.9 | | | | $D_{P2}$, $A_2$ | | |
| 1_5_12 | SH IV | SH05B012_maturity_locus | 0 | | | | | | $c_3$, $D_{P3}$, $A_3$ |
| 199_6_48 | SH VI | EACAMCCT_138.9__6_48 | 61.8 | $t_{m1}$ | $A_{sum}$ | | | | |
| 200_6_56 | SH VI | PAT/MAAC_155.4__6_56 | 73.5 | | $t_1$, $D_{P2}$ | | | | |
| 242_8_29 | SH VIII | PAT/MAAC_283.7__8_29 | 33.2 | | | | | | $D_{P3}$, $A_3$ |
| 291_11_7 | SH XI | EACAMCAC_372__11_7 | 9.2 | | | | | | $t_1$, $c_1$ |
| 47_1_63 | RH IB | EACAMCCT_144.5__1_63 | 27.8 | | | | | | $t_2$, $D_{P2}$, $A_2$ |
| 115_5_4 | RH V | PAC/MAGT_190.2__5_4 | 1.6 | | | | | | $c_3$, $D_{P3}$, $A_3$ |
| 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | $t_1$, $t_2$, $t_e$, $c_{m1}$, $c_1$, $D_{P2}$, $D_{P3}$, $A_2$, $A_3$, $A_{sum}$ | $t_e$, $c_1$, $c_3$, $D_{P2}$, $D_{P3}$, $A_3$, $A_{sum}$ | $t_{m1}$, $t_1$, $t_2$, $t_e$, $v_{max}$, $c_3$, $A_1$, $A_3$, $A_{sum}$ | $t_2$, $t_e$, $c_{m1}$, $c_1$, $D_{P2}$, $A_2$, $A_{sum}$ | $t_2$, $t_e$, $D_{P2}$, $A_2$, $A_{sum}$ | $t_2$, $t_e$, $D_{P2}$, $A_2$, $A_{sum}$ |
| 173_7_68 | RH VII | PAC/MAAC_164.8__7_68 | 21.1 | | | | $c_{m1}$, $c_3$ | | |

This may indicate the difficulties of manipulating correlated traits simultaneously. However, QTLs with similar behaviours could also be interesting targets for breeding programmes as they are more likely to be stable under various environments. Moreover, it is well known that linkage group V harbours the QTL for plant maturity and vigour in potato (Collins et al., 1999; Oberhagemann et al., 1999; Visker et al., 2003; Bradshaw et al., 2008). Our results also confirm this fact as most of our canopy growth and development traits (particularly $A_{sum}$) could be very useful in defining the maturity type in potato (see Chapter 4). Our results give a clear picture that maturity in potato is mainly expressed from the paternal (RH) side. Besides, we also found large number of independent QTLs (i.e. they did not coincide with other traits) (Table 2.11). These QTLs however, with minor effects could be of great value to breeders for further zooming in.

Although many of the QTLs identified were mapped to a similar position in most experiments, most of them were expressed in one environment but not in the other ones (i.e. QTL×E). This was mostly evident for traits ($t_{m1}$, $t_1$, $v_{max}$, $c_{m1}$, $c_1$, $c_3$, $D_{P3}$, $A_1$, and $A_3$) (Table 2.12). For all these traits the G×E component of phenotypic variance was greater than the G variance component (Table 2.3). QTLs controlling such traits often show low stability (Veldboom and Lee, 1996; Reymond et al., 2004). There were marked differences among the environments due to N availability (Table 2.1). Besides, the population was segregating for maturity. Variation in maturity type would be expected to cause variation in a number of the parameters presented (and final yield) because of its relationship with the crop duration (e.g. $t_e$) and its effect on the alignment between crop development processes and environment. These complex interactions might have caused the lower repeatability of many QTLs over the environments due to QTL×E. Several researchers have identified loci that interacted with the environment in different plant species *e.g.*, photoperiod plasticity in Arabidopsis (Ungerer et al., 2003), growth and yield in rice (Hittalmani et al., 2003), flowering phenology in barley (Yin et al., 2005b) and yield in barley (Yin et al., 1999b; Teulat et al., 2001; Voltas et al., 2001).

Only few QTLs were stable across the environments and therefore did not show much of the QTL×E (Table 2.13). For instance, the QTL 116_5_17 on RH V showed up in all the experiments for $A_{sum}$ (Fig. 2.10). Such QTLs could be useful for marker assisted breeding.

**Table 2.11.** List of independent QTLs (i.e. QTLs detected only once for a particular trait in any experiment (environment)).

| QTL | Linkage group | Marker name | Position (cM) | Exp. 1 | Exp. 2 | Exp. 3 | Exp. 4 | Exp. 5 | Exp. 6 |
|---|---|---|---|---|---|---|---|---|---|
| 21_1_32 | SH I | EACAMCAG_381.9__1_32 | 38.7 | | | $v_{max}$ | | | |
| 53_1_32 | SH I | PAC/MAGC_62.6__1_32 | 44.0 | | $A_2$ | | | | |
| 58_1_32 | SH I | PCA/MAAC_211.6__1_32 | 57.8 | | | | $A_1$ | | |
| 67_1_52 | SH I | PAT/MAAC_207.7__1_52 | 80.7 | | | | $t_2$ | | |
| 81_1_92 | SH I | PAC/MACT_132.6__1_92 | 121.9 | | | | $t_2$ | | |
| 102_2_25 | SH II | EAACMCCT_138.3__2_25 | 37.5 | $A_1$ | | | | | |
| 133_4_28 | SH IV | EACTMCTG_74.3__4_28 | 24.8 | | $D_{P2}$ | | | | |
| 265_9_74 | SH IX | PCA/MAGG_294.2__9_74 | 80.9 | | $c_3$ | | | | |
| 293_11_20 | SH XI | PAC/MATA_197.8__11_20 | 21.8 | $t_{m1}$ | | | | | |
| 43_1_35 | RH IA | PAT/MAGT_143.9__1_35 | 58.3 | $A_{sum}$ | | | | | |
| 64_2_21 | RH II | PAG/MACT_230.5__2_21 | 23.5 | | | | | $t_2$ | |
| 79_2_72 | RH II | EACTMCTC_444.3__2_72 | 73.8 | | | | | $A_{sum}$ | |
| 96_4_33 | RH IV | EACAMCAC_156.4__4_33 | 5.5 | | | | $t_1$ | | |
| 101_4_35 | RH IV | EAGAMCAG_216.2__4_35 | 9.6 | | | $t_e$ | | | |
| 98_4_35 | RH IV | EACAMCTG_138.9__4_35 | 12.8 | | $t_1$ | | | | |
| 108_4_72 | RH IV | EAACMCCA_92.1__4_72 | 46.9 | | $t_e$ | | | | |
| 114_5_4 | RH V | EACAMCCT_109.4__5_4 | 4.5 | $A_1$ | | | | | |
| 118_5_42 | RH V | EAACMCCT_201.2__5_42 | 43.9 | | | $A_2$ | | | |
| 153_6_28 | RH VI | PAT/MAAC_272.6__6_28 | 53.8 | | | $t_e$ | | | |
| 154_6_34 | RH VI | EACTMCAG_393.7__6_34 | 59.7 | | | $t_2$ | | | |

**Table 2.12.** Number of QTLs detected across six experiments (environments). Symbol '–' means no QTL was detected.

| Parameter | Exp. 1 | Exp. 2 | Exp. 3 | Exp. 4 | Exp. 5 | Exp. 6 |
|---|---|---|---|---|---|---|
| $t_{m1}$ | 1 | 1 | 1† | – | 2 | – |
| $t_1$ | 1 | 1 | 1† | 2 | – | 1 |
| $t_2$ | 1 | 1 | 2† | 4 | 3 | 2 |
| $t_e$ | 1 | 2 | 3 | 1 | 1 | 1† |
| $v_{max}$ | 1 | – | 3† | 1 | – | – |
| $c_{m1}$ | 1 | – | – | 4† | – | – |
| $c_1$ | 1 | 1 | – | 4† | – | 1 |
| $c_3$ | – | 2 | 1† | – | – | 2 |
| $D_{P2}$ | 1 | 3 | – | 4 | 1† | 2 |
| $D_{P3}$ | 1 | 1† | – | – | 1 | 3 |
| $A_1$ | 2 | 1 | 1† | 1 | – | – |
| $A_2$ | 1 | 1 | 1 | 4 | 1† | 2 |
| $A_3$ | 1 | 1† | 1 | – | 1 | 3 |
| $A_{sum}$ | 2 | 2 | 4† | 3 | 2 | 1 |
| Total QTLs | 15 | 17 | **18** | **28** | 12 | 18 |

† QTLs with maximum additive effects.

**Table 2.13.** List of stable QTLs across six experiments (i.e. Similar QTLs detected in majority of environments).

| QTL | Group | Marker name | Position (cM) | Exp. 1 | Exp. 2 | Exp. 3 | Exp. 4 | Exp. 5 | Exp. 6 |
|---|---|---|---|---|---|---|---|---|---|
| 39_1_32 | SH I | EAACMCCT_217.8__1_32 | 41.6 | | | | × | × | |
| 170_5_44 | SH V | PAC/MAAC_190.2__5_44 | 26.8 | × | | | × | | |
| 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | × | × | × | × | × | × |

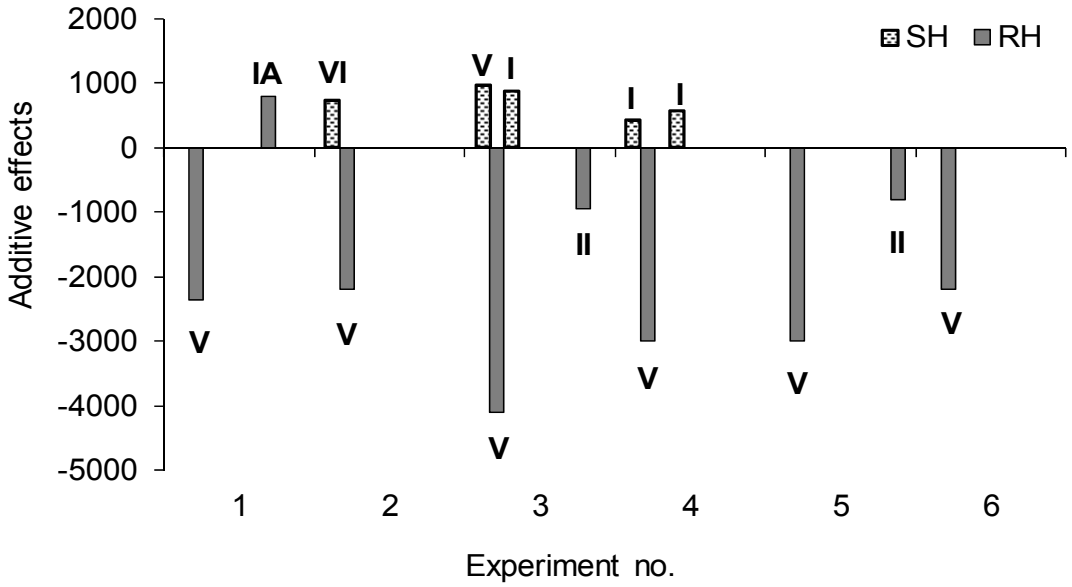


**Figure 2.10.** QTL×E additive effects for total area under canopy curve ($A_{sum}$, *td* %) across paternal (SH and RH) genomes for six experiments. Letters above or below the bars indicate different linkage groups.

## 4. Conclusions

In this study, we presented a quantitative model to describe canopy dynamics of potato. Combined with genetic analysis we aimed to further our knowledge regarding both the genetics and physiology of this trait of potato. The model successfully described the quantitative differences in canopy dynamics of diverse genotypes in a segregating F1 population of potato under varied environments and gave physiological insight using agronomically meaningful traits that characterise canopy formation in potato. These traits are directly related to the ability of the adapted genotypes to intercept photosynthetically active radiation (PAR) and thus to create high tuber yields, as we will show in Chapter 3. In this way, our model approach yielded estimates for agronomically relevant crop characteristics that are useful for defining future breeding strategies in potato.

The scope of crop improvement by breeding is determined by the amount of heritable or genetic variation relative to that of non-heritable or environmental variation, and by the nature and magnitude of G×E interaction which may complicate selection and testing in breeding programmes and result in reduced overall genetic gain. For most traits quantified in the model, considerably high genetic variability along with high heritability were recorded among the F1 population under study. There are opportunities, therefore, to exploit the genetic variability available in the

F1 population and to select for highly heritable traits in order to improve radiation interception efficiency.

In our second analysis, estimated physiological traits were subject to QTL analysis. The AFLP markers were therefore generated for an extended marker map (Fig. 2.9), to which QTL were mapped for the model parameters and derived traits. In total 42 QTLs were identified on both SH and RH parental genomes across all six environments. QTLs with major effects were associated mainly with paternal (RH) linkage group V. One particular QTL (116_5_17) on this linkage group was detected for nearly all traits with a major additive effect and explained most of the total phenotypic variance. Some of the QTLs were mapped to similar positions in majority of the environments. Only few QTLs were stable across the environments and most of them showed QTL×E. The stable QTLs across environments could be useful for marker assisted breeding.

Many researchers identified QTLs for different traits like tuber dormancy (Van den Berg et al., 1996), tuber yield and starch content (Schäfer-Pregl et al., 1998), tuber shape (Van Eck et al., 1994), tuber flesh colour (Bonierbale et al., 1988), tuber skin colour (Gebhardt et al., 1991), yield, agronomic, and quality traits (Bradshaw et al., 2008) in potato under normal conditions. However, knowledge about genetics and physiology of traits related to canopy dynamics and light interception is still limited and hardly any QTLs have been identified for these traits in potato.

Our quantitative approach in combination with markers of the widely available and easy-to-use AFLP marker system identified QTLs that could be useful in the development of marker assisted breeding strategies in potato.

We highlighted the potential of using a model to assist the genetic analysis of quantitative crop trait like canopy cover. Potato models intended for use in yield predictions should first focus on improving genotype-specific estimates of canopy light interception under varied environmental conditions. Research investigations, such as identifying potato canopy characteristics important for breeding trials, can benefit by using our approach to provide an additional level of detail in canopy development.

# CHAPTER 3

## Analysis of genetic variation of potato (*Solanum tuberosum* L.) using standard cultivars and a segregating population. II. Tuber bulking and resource use efficiency*

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**Abstract**

Quantitative differences in the dynamics of tuber bulking of 100 genotypes in a segregating F1 population, their parents (SH, RH) and five contrasting cultivars of potato (*Solanum tuberosum* L.) under various environments were analysed using a piece-wise expolinear function. Tuber bulking was characterised by three parameters: $c_m$, *ED* and $w_{max}$, where $c_m$ and *ED* were growth rate and effective duration, respectively, of the linear phase of tuber bulking, and $w_{max}$ was the final tuber dry weight. We also analysed radiation- and nitrogen-use efficiencies (RUE and NUE, respectively), and their relationships with the model parameters. Values of $c_m$ were highest for early maturing genotypes followed by mid-late and then late genotypes. Late maturing genotypes had longest period of tuber bulking followed by mid-late and early genotypes. As a result $w_{max}$ was higher in late genotypes than in early genotypes. The RUE values were highest for early maturing genotypes followed by mid-late and late genotypes whereas NUE was highest in late maturing genotypes followed by mid-early and early genotypes. Genetic variability and heritability were high for most traits and phenotypic and genetic correlations were high ($r > 0.50$) for these traits as well. Path coefficient analysis showed that RUE, $c_m$, and a previously quantified parameter for total canopy cover $A_{sum}$, had a major influence on $w_{max}$.

Sixteen QTLs were detected for our model parameters and derived traits explaining the phenotypic variance by up to 66%. QTLs controlling most of the traits were on paternal (RH) linkage group V. One particular QTL (116_5_17) on paternal linkage group V at position 18.2 cM was detected for all the traits with a major additive effect and explained most of the total phenotypic variance. Additional QTLs mostly associated with RH linkage groups were detected for traits ($c_m$, $t_E$, and *ED*), whereas both SH and RH linkage groups were associated with traits NUE and $w_{max}$ for minor QTLs. A number of QTLs for traits were not detected when tuber yield *per se* was subjected to QTL analysis. The phenotypic variance explained by the QTLs for tuber yield *per se* was also lower than for other traits. The genetic parameters found in this study indicate that there are opportunities for improving tuber dry matter yield by selection for optimal combination of important physiological traits RUE, $c_m$, and $A_{sum}$.

**Key words:** Potato (*Solanum tuberosum* L.), tuber bulking dynamics, piece-wise expolinear function, components of variance, genotype-by-environment (G×E) interaction, genetic variability, heritability, path coefficient analysis, maturity type, QTL mapping, QTL-by-environment (QTL×E) interaction.

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* *Submitted to Field Crops Research.*

## 1. Introduction

Tuber formation in potato (*Solanum tuberosum* L.) consists of a complex and dynamic sequence of several independently regulated events (Ewing and Struik, 1992; Jackson, 1999), including induction, initiation, set, bulking, and maturation (Vreugdenhil and Struik, 1989). These events are only possible when environment-dependent steps occur in an orchestrated way, including the arrest of stolon growth (Vreugdenhil and Struik, 1989), initiation of radial growth (Catchpole and Hillman, 1969; Mingo-Castel et al., 1976; Struik et al., 1988; Vreugdenhil and Struik, 1989; Ewing and Struik, 1992) and resource storage (Park, 1990; Müller-Röber et al., 1992). The different steps and events can occur independently of each other and are regulated by specific genes (Struik et al., 1999; Kloosterman et al., 2005). The resulting, economically relevant process of tuber bulking is, therefore, regulated by a large set of interacting genes (Bachem et al., 2000).

The onset of tuber bulking greatly impacts subsequent growth, development, and physiology of the entire potato crop (Ewing, 1990, Ewing and Struik, 1992; Van Dam et al., 1996; Walworth and Carling, 2002), because the developing tubers become the dominant sink of both carbon and nitrogen assimilates (Oparka, 1985). The onset of tuber bulking leads to a more or less abrupt preferential partitioning of assimilates to the tubers, thereby causing a reduction in the growth rate and ultimately a complete halting of growth of foliage and roots (Moorby and Milthorpe, 1975; Ewing and Struik, 1992). However, the abruptness depends on the maturity type and other aspects of the genotype-specific physiology (Struik, 2007). Early onset of tuber bulking may result in small plants with limited canopy cover and consequently low final tuber yields, whilst late onset of tuber bulking leads to large plants with high final tuber yields (Bremner and Radley, 1966; Struik, 2007).

Information on the different processes involved and factors affecting plant development and tuber formation in potato are abundant (Ivins and Bremner 1965; Ewing and Struik, 1992; Almekinders and Struik 1996; Kolbe and Stephan-Beckmann, 1997; O'Brien et al., 1998; Jackson, 1999; Struik et al. 1999; Claassens and Vreugdenhil, 2000, and references therein). However, most studies have focused on one or very few of these developmental processes, or on one or a very limited number of genotypes (cultivars). Moreover, the physiological and genetic bases of variability among such traits have not been thoroughly investigated, although some efforts have been made to study the temporal dynamics of important potato developmental processes under diverse environmental conditions on a set of contrasting genotypes. For instance, Spitters (1988) analysed the genotypic differences in tuber bulking of potato on a large set of commercial varieties. Celis-Gamboa et al. (2003) used a highly segregating diploid population of potato to study the temporal relationships

underlying the dynamics of tuber formation and other developmental processes.

Difficulties in manipulating yield are related to its genetic complexity: polygenic nature, interactions between genes (epistasis), and environment-dependent expression of genes (Ribaut and Hoisington, 1998). Many environmental and physical factors, such as temperature, day length, light intensity, water availability, and nitrogen (N), have been demonstrated to influence potato tuberisation (Ewing and Struik, 1992; Jackson, 1999). For example, temperature exerts a major influence on tuberisation and dry matter partitioning to tubers (Ewing, 1981, 1985), with cool air temperatures favouring induction to tuberise (Bodlaender, 1963; Gregory, 1965; Epstein, 1966; Ewing, 1981; Manrique et al., 1984; Struik and Kerckhoffs, 1991), whereas an increase in air temperature may reduce tuber dry matter content and yield (Struik et al., 1989b). Nitrogen also plays a major role in tuberisation (Werner, 1934; Gregory, 1965). Nitrogen helps to attain complete canopy cover early in the season, especially under relatively resource-poor conditions (Haverkort and Rutavisire, 1986; Vos, 2009) and to extend the period of full canopy cover thus leading to increased light interception and tuber yield (Martin, 1995). Radiation is important for dry matter accumulation (Monteith, 1977; Goudriaan and Monteith, 1990) and affects the early processes in tuber formation (Ewing and Struik, 1992) and the rate of tuber bulking (Burstall and Harris, 1983) and its duration. Therefore, resource (radiation, N) use efficiency may have a strong bearing on tuber bulking and final tuber yields.

In our companion paper (Chapter 2), we have quantitatively analysed potato canopy cover dynamics, using a set of varieties covering a wide range of maturity types and a well-adapted diploid F1 segregating population. Here, using the same set of plant materials, we aim to analyse the dynamics of tuber bulking and its variability by breaking them down into biologically meaningful and genetically relevant component traits. We also analyse radiation use efficiency (RUE) and nitrogen use efficiency (NUE) and study their relationships with the tuber bulking traits. We quantify the genetic parameters (variance components and heritability), phenotypic and genetic correlations, and path coefficients of these traits. Finally, we perform QTL mapping of the traits and discuss their genetic basis. The combined information from Chapters 2 and 3 should give insights into the most vital processes that can be used to explore the possibilities of genetically manipulating potato tuber yield.

## 2. Materials and methods

### 2.1. *F1 segregating population of SH × RH and standard cultivars*

The plant material used in this study consisted of 100 F1 diploid (2n = 2x = 24) potato genotypes derived from a cross between two diploid heterozygous potato clones, SH83-92-488 × RH89-039-16 (Rouppe van der Voort et al., 1997; Van Os et al., 2006), or simply the 'the SH × RH population'. The population segregates for maturity type.

Besides the individual F1 genotypes and their two parents, we also included five standard cultivars in our studies: Première, Bintje, Seresta, Astarte, and Karnico. These cultivars were chosen because of their differences in maturity type when grown in the Netherlands, ranging from early (Première) to very late (Karnico). This selection of standard cultivars would allow a benchmarking of consequences of maturity type on the temporal dynamics of tuber bulking. Further information about plant materials is given in Chapter 2.

### 2.2. *Field experiments and measurements*

Six field experiments were carried out in Wageningen (52° N latitude), the Netherlands, during 2002, 2004, and 2005, with two experiments in each year, using the aforementioned plant materials. Details on the methodology and the environmental conditions have been described in Chapter 2. Karnico was not present in the two experiments in 2005.

Tuber dry matter was measured at three harvests during the growing period. The first and second harvests were planned in such a way to measure the tuber dry matter in the linear bulking phase, while the last harvest was performed at maturity. Tubers of each plot were harvested and dried in an oven at 70 °C to constant weight. For samples of the growing seasons of 2004 and 2005, nitrogen (N) concentration in tubers sampled at the end of the growing season was determined by micro-Kjeldahl digestion and distillation (AOAC, 1984). Total amount of N in tubers was calculated from the N concentration and tuber dry weight.

### 2.3. *A model for tuber bulking dynamics*

Like the life cycle of any plant or its organ, potato tuber growth as a function of time follows a sigmoid pattern, including an early accelerating phase, a linear phase and a ripening phase (Fig. 3.1). We used the expolinear function of Goudriaan and Monteith (1990) to describe the tuber growth during the exponential phase:

$$w = \frac{c_m}{r_m}\ln\left[1 + e^{r_m(t-t_B)}\right] \quad \text{with } t \le t_B \tag{3.1}$$

where $w$ is tuber mass, $t$ is time, $t_B$ is the moment at which the linear phase of tuber bulking effectively begins, $r_m$ is the relative growth rate in the 'exponential phase', and $c_m$ is the growth rate in the 'linear phase'.

Eqn (3.1) can, in principle, be used to describe the tuber growth of the linear phase as well. However, eqn (3.1) tends to under-estimate the true growth rate because of its curvilinear nature. To obtain an objective estimation of the growth rate of the linear phase, we used the following linear model to quantify the second phase:

$$w = w_B + c_m(t - t_B) \quad \text{with } t_B < t < t_E \tag{3.2}$$

where $t_E$ is the end time of the linear phase, $w_B$ is the tuber weight at time $t_B$. If we know $r_m$ and $c_m$, then $w_B$ can be estimated from eqn (3.1) as 0.693 $c_m/r_m$.

To represent a deflection in growth towards the third phase, Goudriaan and Monteith (1990) suggested a truncated curve that terminates growth at the time $t_E$, when the maximum weight ($w_{max}$) is achieved. This is a brutal method, because growth stops gradually rather than abruptly. However, given the limited number of measurements in the time series (see above), we adopted the truncated curve approach, with:

$$w = w_{max} \quad \text{with } t \ge t_E \tag{3.3}$$

where $t_E$ is calculated as $t_B + (w_{max} - w_B)/c_m$.

Combining eqns (3.1, 3.2, and 3.3) yields a model with four parameters: $r_m$, $c_m$, $t_B$, and $w_{max}$, while the two other parameters $w_B$ and $t_E$ are calculated as 0.693 $c_m/r_m$ and $t_B + (w_{max} - w_B)/c_m$, respectively. Obviously an over-fitting would be obtained if all the four parameters were to be directly fitted from our limited data points for each genotype. Ingram and McCloud (1984) and Van Dam et al. (1996) reported that $r_m$ was conservative across potato cultivars at a given temperature. Their $r_m$ value 0.34 $d^{-1}$ at the optimum temperature was used here for all genotypes. We also fixed parameter $w_{max}$ as the average of two blocks of the final measured weight. The two remaining parameters (i.e. $c_m$, $t_B$) can be estimated, but with the value of $t_B$ having large standard error, probably due to insufficient data points for the early season. Using these estimated values, we found that the initial weight ($w_0$) at time zero, calculated using eqn (3.1), did not vary much across genotypes. We, therefore, used the value for $w_0$ = 0.13 (g $m^{-2}$), the averaged $w_0$ across all six

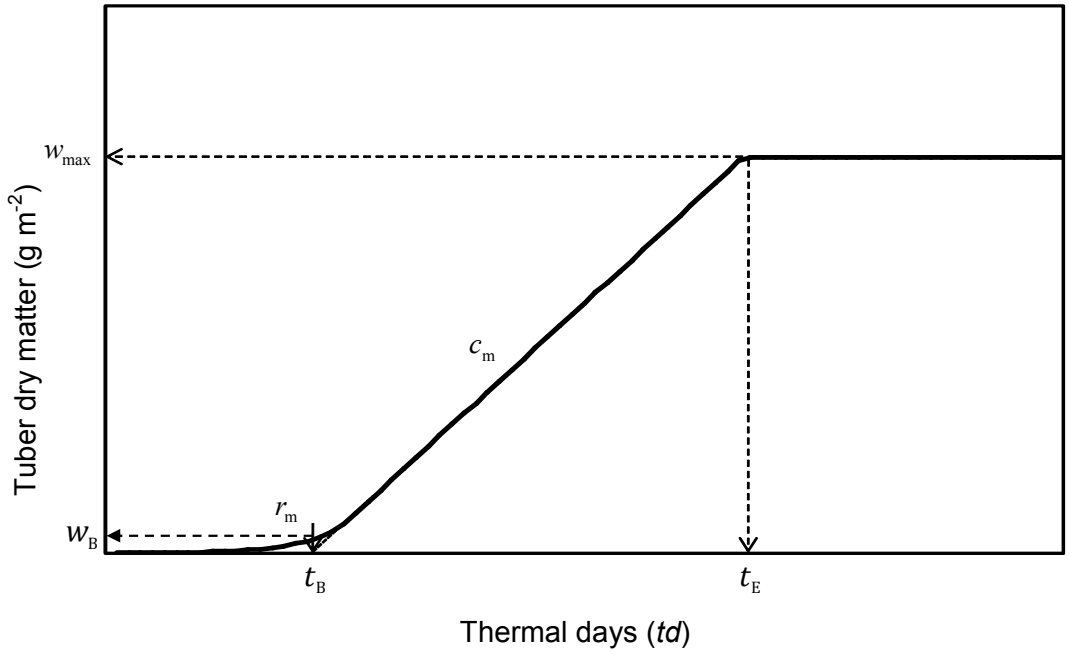


**Figure 3.1.** Tuber bulking dynamics in potato represented by the piece-wise expolinear growth function.

experiments and all genotypes, to further reduce the number of parameters to be estimated. When $w_0$ is fixed, parameter $t_B$ can be calculated from eqn (3.1) as:

$$t_B = -\frac{1}{r_m}\ln\left(e^{\frac{w_0 r_m}{c_m}} - 1\right) \qquad (3.4)$$

This is in accordance with Goudriaan (1994), who suggested that it may be a more natural sequence to express $t_B$ as a function of initial weight ($w_0$) at emergence.

Eqn (3.4) and the formulae for calculating $w_B$ and $t_E$, were combined with eqns (3.1-3.3), for curve fitting. The fitting was performed for each genotype of every experiment with the iterative non-linear least-square regression using the Gauss method, as implemented in the PROC NLIN of the SAS software (SAS Institute Inc., 2004). Obviously, our procedure estimated only $c_m$, which together with $w_{max}$ as primary model parameters, characterises genotypic and environmental effects on tuber growth. Parameters $t_B$, $t_E$, and $w_B$ were calculated from the equations described earlier. The effective duration of tuber bulking (*ED*), an additional useful trait, was calculated as $t_E - t_B$.

As in our first analysis for canopy cover (Chapter 2), all time variables and

duration were expressed as thermal days (*td*) to account for the influence of daily and seasonal temperature fluctuations on tuber growth. The method for conversion of the actual days into *td* was given by Yin et al. (2005) and its application to our potato genotypes has been described in Chapter 2. Note that the *td* is equal to or smaller than the number of chronological days.

### 2.4. *Calculation of Radiation Use Efficiency (RUE)*

The radiation use efficiency (RUE; g DM $MJ^{-1}$ $PAR_{int}$) was estimated for each individual plot by dividing the total tuber dry matter at maturity (g DM $m^{-2}$) by the cumulative intercepted photosynthetically active radiation (MJ $PAR_{int}$ $m^{-2}$) for the entire growth period. Data of incident global solar radiation were obtained from a weather station in Wageningen located nearby the experimental sites. Daily incident PAR was calculated as half of the global solar radiation (Spitters, 1988). To calculate cumulative $PAR_{int}$, our extensive data on the percentage green canopy cover (Chapter 2) were converted to PAR-interception percentage, using a linear relationship given by Burstall and Harris (1983) as $PAR_{int}$ (%) = 0.956×canopy cover (%) – 4.95. Daily values of $PAR_{int}$ were summed and the obtained cumulative $PAR_{int}$ was used to calculate seasonal average RUE on the tuber-dry weight basis.

### 2.5. *Calculation of Nitrogen Use Efficiency (NUE)*

As we did not measure dry weight and N content in the organs other than tubers, nitrogen use efficiency (NUE; g DM $g^{-1}$ N) was expressed on the tuber dry matter basis, as was RUE, by dividing the total tuber dry matter (g DM $m^{-2}$) by total tuber nitrogen uptake (g N $m^{-2}$). This way of presenting NUE means that NUE is mathematically equivalent to the inverse of tuber N concentration (g N $g^{-1}$ DM).

### 2.6. *Statistical and genetic analysis*

All statistical analyses were performed in Genstat (Payne et al., 2009). Combined analysis of variance across experiments (i.e. environments) was performed to test the significance and extent of differences among environments and genotypes (including the F1 population, the parents, and standard cultivars). Means of genotype and environment terms were compared using the Fisher's least significant difference (LSD) test. Further statistical analyses were performed only using the F1 population means (100 genotypes) across six environments as described below.

### 2.6.1. Estimation of variance components

The variance components for genetic, environmental and experimental error were estimated through the REML procedure to assess their contribution to the total phenotypic variance of the traits $c_m$, $t_E$, *ED,* RUE, NUE, and $w_{max}$. Significance levels were determined with a likelihood ratio test (Morrell, 1998), which tests the change in deviation after removing the respective variance component from the model. The change in deviation is approximately chi-square distributed (Littell et al., 1996). Once these variance components were estimated, phenotypic variance ($\sigma^2_{Ph}$) was calculated as per following equation (Bradshaw, 1994; Falconer and Mackay, 1996; Lynch and Walsh, 1998):

$$\sigma^2_{Ph} = \sigma^2_G + \sigma^2_E + \sigma^2_\varepsilon \quad (3.5)$$

where $\sigma^2_G$ is genetic variance, $\sigma^2_E$ represents environmental variance, and $\sigma^2_\varepsilon$ is experimental error variance.

### 2.6.2. Phenotypic and genetic coefficients of variation

Coefficients of variation (%) were calculated according to the following equation:

$$CV_X = \frac{\sqrt{\sigma^2_X}}{\mu} \times 100 \quad (3.6)$$

where $\mu$ is the grand mean of the population, and $\sigma^2_X$ is a variance component (i.e. $\sigma^2_{Ph}$ or $\sigma^2_G$ or $\sigma^2_E$).

### 2.6.3. GGE biplot analysis

GGE biplot analysis was performed to analyse the inter-relations among genotypes and environments. GGE biplots were constructed by plotting the first principal component (PC1) scores of the genotypes and the environments against their respective scores for the second principal component (PC2). The environment-standardised method of Yan (2002) was used.

### 2.6.4. Heritability

Estimates of broad-sense heritability ($H^2$) (%) were calculated by using the estimated variance components (Falconer and Mackay, 1996; Holland et al., 2003):

$$H^2 = \frac{\sigma_G^2}{\sigma_G^2 + \frac{\sigma_\varepsilon^2}{n_t}} \times 100 \quad (3.7)$$

where ($n_t$ = 6) is the product of number of blocks and environments.

### 2.6.5. Phenotypic and genetic correlation

Phenotypic correlations were calculated using the Pearson Correlation Coefficient. The genetic correlations were calculated using the following equation (Holland, 2006):

$$r_{Gij} = \frac{\sigma_{Gij}^2}{\sqrt{\sigma_{Gi}^2 \sigma_{Gj}^2}} \quad (3.8)$$

where $\sigma^2_{Gij}$ is the estimated genetic covariance between traits *i* and *j*; $\sigma^2_{Gi}$ and $\sigma^2_{Gj}$ are the genetic variances of traits *i* and *j*, respectively. The variance and covariance components were estimated from multivariate REML analyses (Meyer, 1985; Holland, 2006). The significance of genetic correlations was determined using a *t*-test after a *z*-transformation of the correlation coefficients (Sokal and Rohlf, 1995; Gutteling et al., 2007).

### 2.6.6. Path coefficient analysis

The inter-associations between the important yield determining components were ascertained across all six experiments by working out the path coefficient analysis following the procedure of Dewey and Lu (1959). This was accomplished by partitioning the direct and indirect effects of various physiological traits upon the final tuber dry matter. The final tuber dry matter (i.e. $w_{max}$) was considered as the response variable while traits $c_m$, *ED*, $A_{sum}$, RUE, and NUE were assumed to be the predictor variables, where $A_{sum}$ is the area under the whole canopy-cover curve and reflects the capability of the crop to intercept solar radiation during the whole growing season, as quantified in Chapter 2. The direct effects of predictor variables were the path coefficients computed through multiple regression. A path coefficient is a standardized regression coefficient (Li, 1975). Indirect effects were computed as the product of the correlation coefficient between two variables and the path

coefficient from the second variable to the response variable. Let variables $x_1$ to $x_5$ refer to $c_m$, *ED*, $A_{sum}$, RUE, and NUE, respectively. The total effect of a predictor variable $x_1$ correlated with other predictor variables $x_2$, $x_3$, $x_4$, and $x_5$ on response variable z, would be given by, for example:

$$r_{zx1} = P_{zx1} + (P_{zx2} \times r_{x1x2}) + (P_{zx3} \times r_{x1x3}) + (P_{zx4} \times r_{x1x4}) + (P_{zx5} \times r_{x1x5}) \quad (3.9)$$

where $r_{zx1}$ is total correlation between z and $x_1$, $P_{zx1}$ represents path coefficient from $x_1$ to z $r_{x1xi}$ (i =2, 3, 4 and 5) is correlation coefficient between variables $x_1$ and $x_i$, and $P_{zxi}$ denotes path coefficient from $x_i$ to z. The same logic was applied to compute $r_{zx2}$, $r_{zx3}$, ..., $r_{zx5}$.

### 2.6.7. QTL detection

The parental (SH, RH) genetic map described in Chapter 2 was used for QTL mapping of traits. Eighty-eight genotypes of our 100 F1 lines were covered in the extended ultra-dense genetic map of 250 lines of SH × RH population (cf. Chapter 2); data of these 88 lines were therefore used for detection of QTLs for model parameters, derived traits and (N, radiation) use efficiencies. QTL analysis was done individually for all six experiments (environments) using Genstat version 14 (Payne et al., 2009) software. For more details about the mapping procedure, see Materials and Methods of Chapter 2.

## 3. Results and discussion

### 3.1. *Model performance in describing tuber bulking dynamics of genotypes*

The model for tuber bulking dynamics (i.e. combined eqns 3.1-3.3) fitted well for each genotype of the potato segregating population, the parents and the standard cultivars in the entire data set, with $R^2$ values ranging from 0.90 to 1.00 (n = 6). The estimated tuber bulking curves for the two parents (SH and RH) and four standard cultivars are shown in Fig. 3.2. The transformation of calendar days into thermal time resulted in a more stable parameter estimation (data not shown), as thermal time effectively removed the confounding effect of diurnal and seasonal temperature fluctuations during the experimental period. Overall, combined eqns (3.1-3.3) are very useful in analysing the tuber bulking dynamics of a diverse set of potato genotypes under various environments.

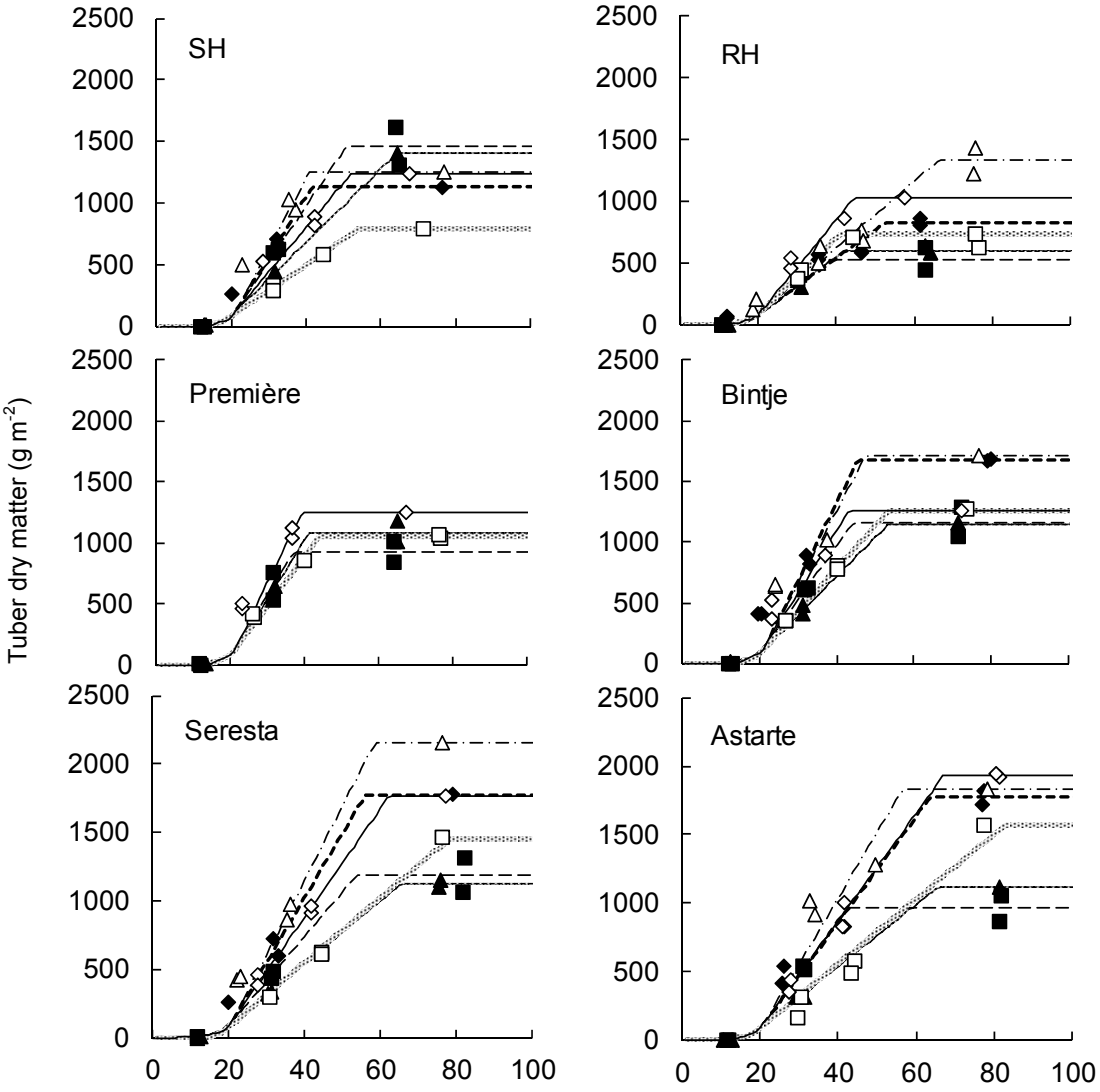


**Figure 3.2.** Observed (obs) points and fitted (fit) curves of parents (SH and RH) and four standard cultivars for all six experiments (environments).

### 3.2. *Model parameters and secondary traits*

Results of combined analysis of variance showed highly significant ($P$<0.01) effects of genotype (including 100 F1 genotypes, the parents, and standard cultivars) across the experimental sites (i.e. environments) on all model parameters and derived traits. However, as expected, differences between cultivars and across environments in the onset of tuber bulking ($t_B$) were very small, because as mentioned earlier $t_B$ was calculated by eqn (3.4) where $w_o$ and $r_m$ were fixed due to limited data points for the early growth phase. Similarly, the tuber weight ($w_B$) achieved at $t_B$ was calculated in relation to $r_m$ and $c_m$ (see Materials and Methods). Therefore, we will no longer analyse the variation of $t_B$ and $w_B$.

There were significant differences ($P$<0.05) among the standard cultivars for $c_m$, $t_E$, *ED*, and $w_{max}$ (Table 3.1). Values of $c_m$ were comparatively higher for early maturing cultivars like Première and mid-early cultivars like Bintje than for late ones like Astarte and Karnico.

The values for $t_E$ and *ED* were higher for late maturing cultivars than for mid-late and early cultivars. The maximum tuber dry matter yield ($w_{max}$), on the other hand was higher for late maturing cultivars than for mid-late and early cultivars. The higher values of $w_{max}$ in late maturing cultivars might be due to their comparatively higher $t_E$ and longer *ED*. This is in line with the result of Kooman and Rabbinge (1996), who found that compared with late cultivars, early potato cultivars allocate a larger part of the available assimilates to the tubers early in the growing season, resulting in shorter growing periods and also lower yields. Moreover, cultivars differences with respect to tuber yielding potential could be attributed to variation in efficiency of assimilate partitioning to the tubers (bulking rate) and maturity period. Hammes and De Jager (1990) and Gawronska et al. (1990) reported the existence of varietal differences with respect to the rate of net photosynthesis and dry matter production.

Table 3.2 shows trait values of the F1 segregating population in comparison with their parents (SH and RH). The means of the F1 segregating population were not within the ranges of the parental clones for parameters $t_E$ and *ED*. Wide ranges were observed for all model parameters and derived traits. Most of the parameters were

**Table 3.1.** Estimated mean values of different traits for five standard cultivars (listed in order of increasingly longer crop cycle), as obtained from combined ANOVA across six environments. *td* stands for thermal day.

| Cultivar | $c_m$ (g DM $td^{-1}$) | $t_E$ (*td*) | *ED* (*td*) | RUE (g DM $MJ^{-1}$) | NUE (g DM $g^{-1}$ N) | $w_{max}$ (g DM $m^{-2}$) |
|---|---|---|---|---|---|---|
| Première | 55.7 a | 37.3 c | 16.1 c | 2.7 a | 70.4 c | 1122 b |
| Bintje | 48.2 ab | 47.9 b | 27.4 b | 2.4 a | 72.1 c | 1375 ab |
| Seresta | 36.7 bc | 62.4 a | 42.8 a | 2.4 a | 88.5 b | 1579 a |
| Astarte | 35.4 bc | 63.0 a | 43.5 a | 2.2 ab | 90.9 b | 1533 a |
| Karnico | 31.2 c | 63.7 a | 44.4 a | 1.9 b | 101.8 a | 1487 a |
| LSD ($P$<0.05) | 13.2 | 10.1 | 10.7 | 0.5 | 7.7 | 263 |

Means within a column followed by different letters are significantly different according to Fisher's Multiple Range Test ($P$<0.05).

nearly normally distributed displaying transgressive segregation (Fig. 3.3).

Environment had highly significant ($P$<0.01) effects on all model parameters and derived traits. There were significant differences ($P$<0.05) between the experiments for $c_m$, $t_E$, *ED*, and $w_{max}$ (Table 3.3), within five standard cultivars. This was at least partly due to the purposeful variation in availability of N across trials (Chapter 2). Figure 3.4 illustrates the variation (the median, minimum and maximum values) of these model parameters and derived traits for the F1 population per individual experiment. The ranges of the parameters $c_m$, and $w_{max}$ were consistently wider in Exp 3 than in the other experiments (Fig. 3.4). In case of $t_E$ and *ED*, wider ranges were observed in Exps 4 and 5, respectively (Fig. 3.4). This could be attributed to varied availability of N per experiment (Chapter 2) in interaction with genotype specific behaviour, causing different trade-offs between rate and duration of tuber bulking and tuber final dry matter production.

### 3.3. *Radiation Use Efficiency (RUE)*

The RUE differed significantly ($P$<0.01) among the genotypes (standard cultivars and F1 segregating population). The values of RUE ranged between 1.9 and 2.7 g DM $MJ^{-1}$ (Table 3.1). The calculated values of RUE were within the range reported in the literature for *Solanum tuberosum* genotypes under temperate conditions (Spitters, 1988; Scott and Wilcockson, 1978; Allen and Scott, 1980; Khurana and McLaren, 1982; MacKerron and Waister, 1985a; Stol et al., 1991; Kooman and Haverkort, 1995).

**Table 3.2.** Estimated mean values of different traits (across six environments) for two parents (SH and RH) and mean, minimum (Min), maximum (Max), and range within the F1 population. *td* stands for thermal day.

| Parameter | SH | RH | ‡Mean (±S.E.) | Min | Max | Range |
|---|---|---|---|---|---|---|
| $c_m$ (g $td^{-1}$) | 39.8 | 29.0 | 35.5 (±4.2) | 19.9 | 47.4 | 27.5 |
| $t_E$ (*td*) | 50.8 | 46.9 | 51.0 (±2.9) | 42.5 | 62.9 | 20.4 |
| *ED* (*td*) | 30.9 | 27.8 | 31.8 (±3.3) | 22.4 | 45.1 | 22.7 |
| RUE (g DM $MJ^{-1}$) | 2.7 | 2.4 | 2.1 (±0.2) | 1.5 | 2.6 | 1.1 |
| NUE (g DM $g^{-1}$ N) | 69.6 | 67.2 | 68.2 (±5.6) | 54.4 | 81.6 | 27.2 |
| $w_{max}$ (g $m^{-2}$) | 1219 | 847 | 955.6 (±50.0) | 830.4 | 1115.7 | 285.3 |

‡ Mean of F1 segregating population (100 genotypes) across six environments.

**Table 3.3.** Estimated mean values of different traits for each individual environment as obtained from combined ANOVA across five standard cultivars. *td* stands for thermal day.

| Parameter | Exp. 1 | Exp. 2 | Exp. 3 | Exp. 4 | Exp. 5 | Exp. 6 | LSD |
|---|---|---|---|---|---|---|---|
| $c_m$ (g $td^{-1}$) | 30.6 d | 41.6 c | 46.1 b | 50.0 a | 30.9 d | 48.3 a | 2.2 |
| $t_E$ (*td*) | 55.4 d | 42.9 f | 61.1 b | 59.4 c | 64.6 a | 53.0 e | 1.7 |
| *ED* (*td*) | 36.3 d | 22.8 f | 40.8 b | 38.8 c | 45.5 a | 32.5 e | 1.8 |
| RUE (g DM $MJ^{-1}$) | 2.1 d | 2.0 e | 2.8 a | 2.6 b | 2.0 e | 2.4 c | 0.09 |
| NUE (g DM $g^{-1}$ N) | – | – | 102.5 a | 80.8 c | 69.4 d | 84.8 b | 1.5 |
| $w_{max}$ (g $m^{-2}$) | 1086 e | 1003 f | 1834 b | 1954 a | 1341 d | 1555 c | 44 |

Means within a row followed by different letters are significantly different according to Fisher's Multiple Range Test ($P$<0.05).

Significant ($P$<0.05) differences were observed among the standard cultivars with respect to RUE. The RUE values were comparatively high for early and mid-early cultivars (Première and Bintje, respectively) followed by mid-late (Seresta) and late cultivars (Karnico). These results were expected because cumulative light absorption tended to be greater for the later maturing cultivars, but on the other hand, they exhibited a smaller harvest index (data not shown). Owing to these opposite trends for cumulative light absorption and harvest index, tuber yield showed an optimum relationship with maturity class. Early maturing cultivars allocate already in an early phase the major part of their current assimilates to tuber growth, which is at the expense of canopy growth (Spitters, 1988). Senescence of leaves, without significance formation of new leaves, causes an early senescence of foliage. Early cultivars had, therefore, a smaller cumulative light absorption but a greater harvest index and RUE. On the other hand, late maturing cultivars maintain green, active foliage for an extended period of time (Spitters and Schapendonk, 1990). However, the investment in canopy growth is at the expense of tuber growth.

Table 3.2 compares the mean, and ranges of RUE between the two parents (SH and RH) and F1 segregating population. RUE values varied from 2.7 g DM $MJ^{-1}$ for SH and 2.4 g DM $MJ^{-1}$ for RH parent, compared with mean (2.1 g DM $MJ^{-1}$) of F1 population. The mean RUE of F1 population was lower than the value of either parent, but this was associated with a wide variation in the population for RUE with values ranging from 1.5 g DM $MJ^{-1}$ to 2.6 g DM $MJ^{-1}$ (Table 3.2) and therefore displayed transgressive segregation (Fig 3.3). There are possibilities therefore for the breeders to exploit this variation for improving RUE.

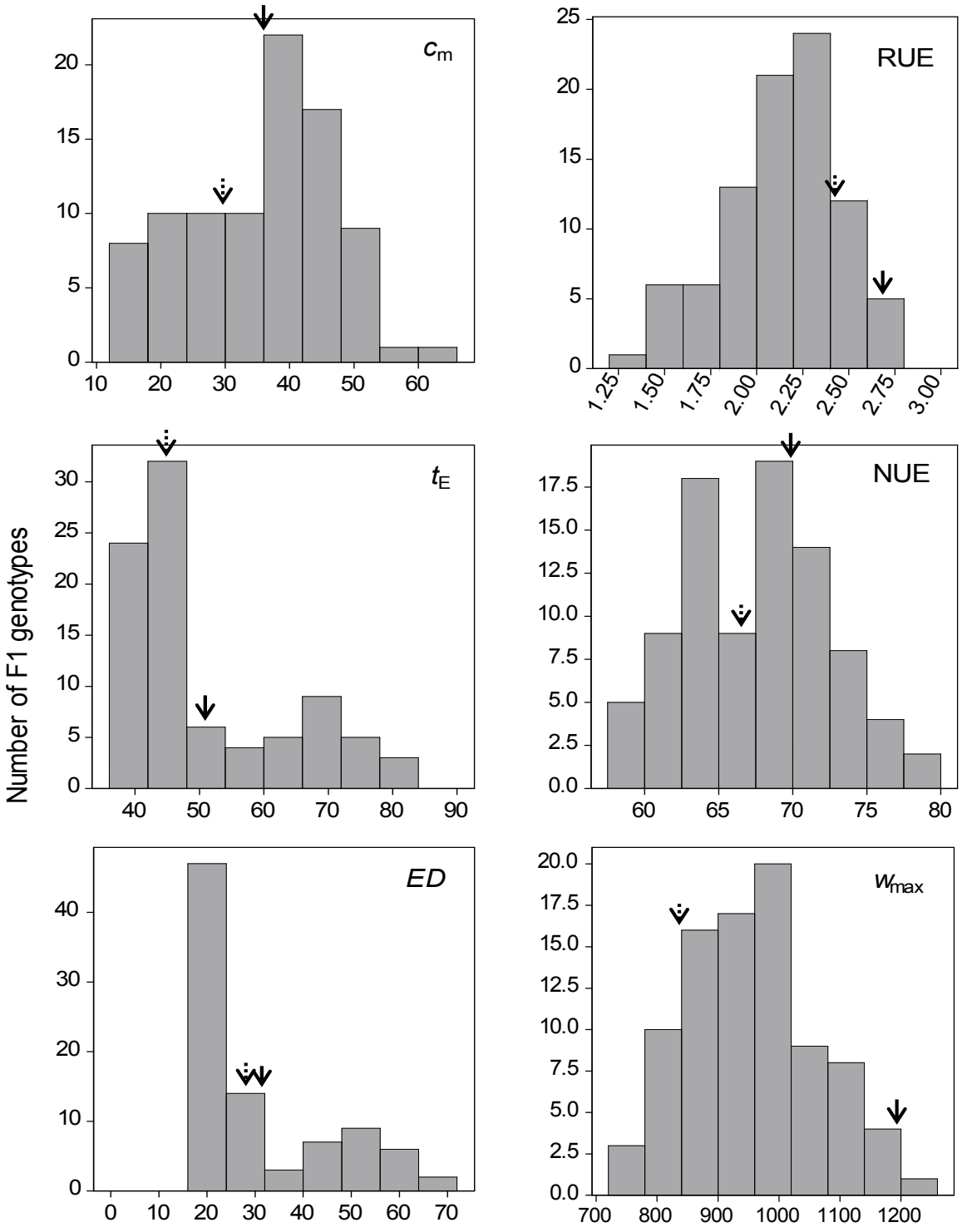


**Figure 3.3.** Distribution of five model parameters among F1 genotypes across six experiments (environments). The values of two parents 'SH' and 'RH' are indicated by full arrow and dashed arrow, respectively.

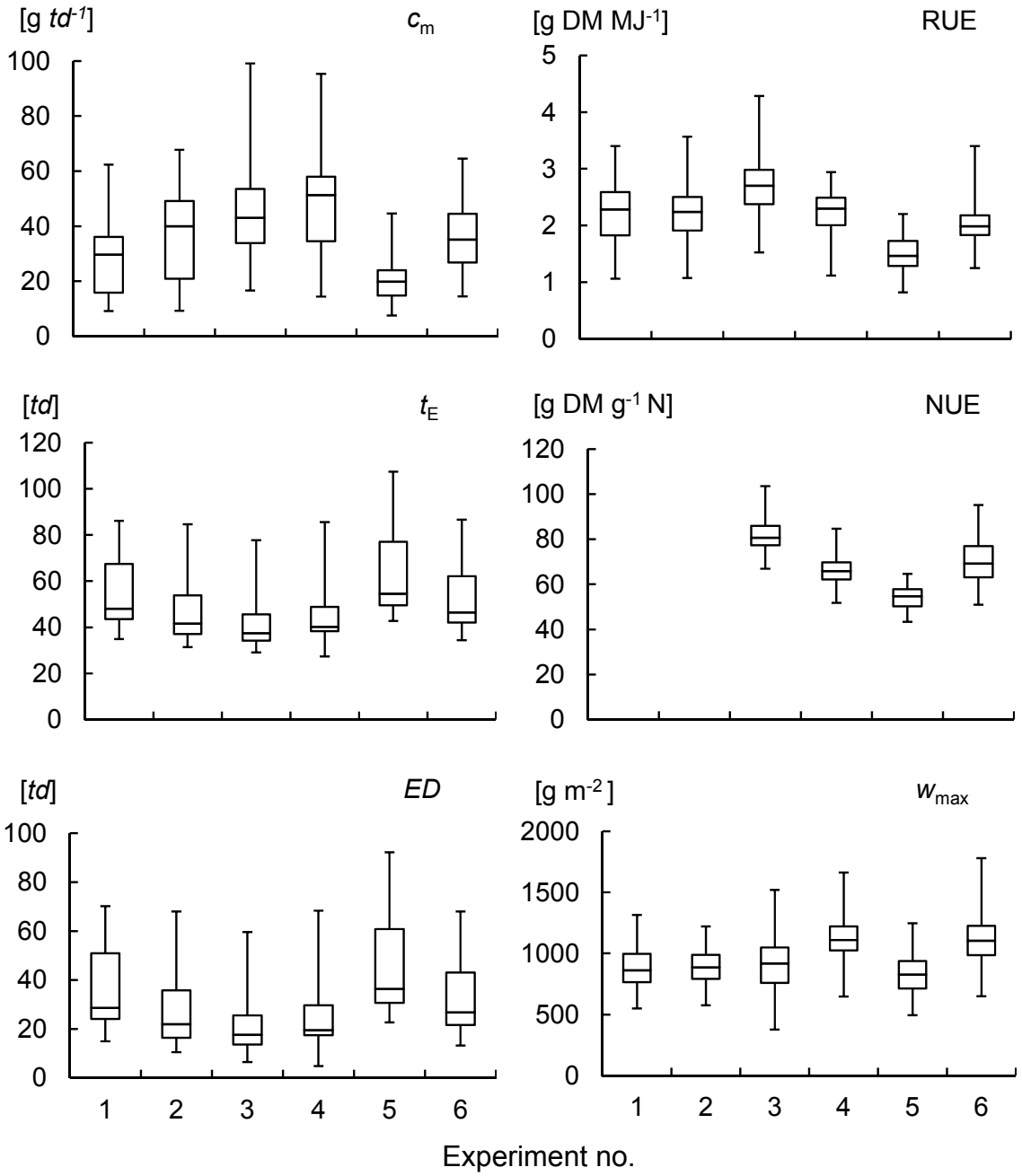


**Figure 3.4.** Box plots of genetic means of an F1 population of different traits in all six experiments. The boxes span the interquartile range of the trait values, so that the middle 50% of the data lay within the box, with a horizontal line indicating the median. Whiskers extend beyond the ends of the box as far as the minimum and maximum values.

The RUE showed significant ($P$<0.05) variation amongst environments for the set of standard cultivars as well as for the F1 segregating population. For the standard cultivars RUE mean values were higher in Exp 3 and lower in Exp 5 (Table 3.3). For the F1 population a similar trend was observed with wider and lower ranges of variation in Exp 3 and Exp 5, respectively (Fig. 3.4) than in the other experiments. We surmise that such within and between experimental variations are the combined result of differences in $A_{sum}$ associated with variation in maturity class and with varied availability of N (Chapter 2). Plant nitrogen status and crop growth cycle both affect RUE, in addition to the effects of other factors (Green, 1987; Muchow and Davis, 1988; Sinclair and Horie, 1989; Trapani et al., 1992).

The RUE has been used to explain genotypic differences in potato under diverse environments (Sibma, 1970, 1977; Van der Zaag and Burton, 1978; MacKerron and Waister, 1985a; Van der Zaag and Doornbos, 1987; Vander Zaag and Demagante, 1987; Trebejo and Midmore, 1990; Koman et al., 1996). Van der Zaag and Doornbos (1987) concluded from their trials with 19 cultivars that cultivar differences in tuber dry matter yield were mainly due to variation in RUE under varied growing conditions. It is concluded that analysis of yield variation between potato genotypes can be obtained by interpreting that variation in terms of accumulated light absorption, average RUE, and harvest index.

### 3.4. *Nitrogen Use Efficiency (NUE)*

Highly significant ($P$<0.01) effects of genotype (standard cultivars and F1 segregating population) were observed for NUE (data not shown). Mean estimates for NUE ranged between 69.6 to 101.8 g DM $g^{-1}$ N (Table 3.1). NUE varied significantly ($P$<0.05) among the standard cultivars. NUE values were comparatively higher for late maturing cultivars like Karnico and Astarte than for mid-early and early cultivars such as Bintje and Première, respectively (see also Zebarth et al., 2004). These effects were mainly associated with differences in maturity type (Van Kempen et al., 1996). Late maturing cultivars combine a long canopy cover with a long tuber bulking period ($ED$) and therefore achieve more tuber dry matter yield ($w_{max}$) per unit of N uptake than mid early and early maturing cultivars (Zebarth et al., 2008). Previous research has also demonstrated that there is significant variation in crop uptake and use efficiency of N among commercial potato cultivars and advanced clones (Kleinkopf et al. 1981; Lauer 1986; Sattelmacher et al., 1990; Porter and Sisson, 1991a,b; Johnson et al. 1995; Errebhi et al., 1998a,b, 1999; Sharifi et al., 2007; Zebarth et al., 2004, 2008).

Mean comparison of NUE between two parents (SH and RH) and within the F1 population is given by (Table 3.2). NUE in the F1 population was, on average, 68.2 g

DM $g^{-1}$ N which was close to the values of the two parents (SH: 69.6 g DM $g^{-1}$ N; RH: 67.2 g DM $g^{-1}$ N). However, there was a very wide variation in NUE within the F1 population; it ranged from 54.4 g DM $g^{-1}$ N to 81.6 g DM $g^{-1}$ N. This wide range suggested a transgressive segregation in F1 population for NUE (Fig. 3.3), which could be further genetically manipulated for improving N use efficiency characteristics in potato.

There was significant ($P$<0.05) variation in NUE among the six environments for the standard cultivars (Table 3.3), as well as for the F1 segregating population (Fig. 3.4); trends were consistent for the two groups of genotypes. The highest NUE was recorded in Exp 3 and the lowest in Exp 5, in line with lower tuber N uptake (11.3 g $m^{-2}$) observed in Exp 3 and higher tuber N uptake (15.3 g $m^{-2}$) observed in Exp 5 (Chapter 2). Responses to N can vary greatly from site to site and from year to year. They depend on the capacity of the soil to supply N when the crop needs it (Meyer, 1998) and on the capacity of the crop to make efficient use of that N.

The NUE also varied within the experiments, with wide ranges of variation observed in Exp 6 (Fig. 3.4). This might be due to the indirect effects of different maturity groups within the F1 population. The different durations of the crop cycle, as expressed by maturity classes, is an obvious factor one might expect to affect the N response too (Vos, 2009).

### 3.5. *Phenotypic, genetic and environmental variances*

Table 3.4 presents estimated values of phenotypic, genetic and environmental variances for all the parameters and the derived traits in the F1 population. The results revealed considerable phenotypic and genetic variances for all the traits studied. All genetic and environmental components of variation were significant ($P$<0.01) (Table 3.4).

The genetic variance component contributed a major portion to the phenotypic variance in traits $c_m$, $t_E$, and $ED$ (Table 3.4). The contribution of the environmental variance to the phenotypic variance was relatively large in $w_{max}$, RUE, and NUE (Table 3.4), probably because these traits were sensitive to nitrogen as we purposefully applied varied doses of nitrogen for creating contrasting environments (see Materials and Methods, Chapter 2). A number of studies have also shown a varying response to rates of N on the dry matter yield production in potato crops (e.g. Porter and Sisson, 1991b; Maier et al. 1994; Feibert et al. 1998; Belanger et al. 2000).

Estimates of phenotypic ($CV_{Ph}$) and genetic ($CV_G$), and environmental ($CV_E$) coefficients of variation for traits across the six experiments are presented in Table 3.5. Estimates of $CV_{Ph}$ ranged from 19.5% to 54.7%. These estimates were

**Table 3.4.** Variance components for different traits within the F1 population across all six experiments.

| Parameter | $\sigma^2_{Ph}$ | $\sigma^2_E$ | $\sigma^2_G$ | $\sigma^2_\varepsilon$ |
|---|---|---|---|---|
| $c_m$ (g $td^{-1}$) | 297.5 | 107.6** | 120.6** | 69.2 |
| $t_E$ ($td$) | 253.9 | 51.1** | 169.1** | 33.7 |
| $ED$ ($td$) | 301.0 | 65.1** | 197.3** | 38.6 |
| RUE (g DM $MJ^{-1}$) | 0.34 | 0.15** | 0.09** | 0.10 |
| NUE (g DM $g^{-1}$ N) | 177.2 | 125.9** | 20.7** | 30.6 |
| $w_{max}$ (g $m^{-2}$) | 47025 | 14706** | 9902** | 22417 |

** Significant at 1%.

$\sigma^2_{Ph}$ = phenotypic variance, $\sigma^2_E$ = environmental variance, $\sigma^2_G$ = genetic variance, $\sigma^2_\varepsilon$ = residual variance.

smallest for NUE and highest for *ED*. Traits with high $CV_{Ph}$ exhibit large total variance and are useful as selection criteria in breeding provided the trait is also heritable. The $CV_G$ estimates were higher than $CV_E$ estimates for all traits investigated. However, the ratio of $CV_G$ over $CV_E$ was much greater in traits NUE, $t_e$, and *ED*, followed by RUE and $w_{max}$, whereas the lowest ratios were observed in $c_m$. Our results indicated that significant genetic variability existed within the F1 population for most traits. It is therefore possible to utilise this wide genetic variability available for a breeding programme aimed at improving tuber bulking dynamics, RUE, NUE, and ultimately tuber dry matter production.

**Table 3.5.** The phenotypic coefficient of variation ($CV_{Ph}$ ), genetic coefficient of variation ($CV_G$), environmental coefficient of variation ($CV_E$), and broad-sense heritability ($H^2$) of different traits within the F1 population across all six experiments.

| Parameter | ¶Mean | $CV_{Ph}$ (%) | $CV_G$ (%) | $CV_E$ (%) | $H^2$ (%) |
|---|---|---|---|---|---|
| $c_m$ (g $td^{-1}$) | 35.5 | 48.6 | 30.9 | 29.2 | 91.3 |
| $t_E$ ($td$) | 51.0 | 31.3 | 25.5 | 14.0 | 96.8 |
| $ED$ ($td$) | 31.7 | 54.7 | 44.3 | 25.5 | 96.8 |
| RUE (g DM $MJ^{-1}$) | 2.1 | 27.1 | 17.9 | 13.9 | 84.2 |
| NUE (g DM $g^{-1}$ N) | 68.1 | 19.5 | 16.5 | 6.7 | 80.2 |
| $w_{max}$ (g $m^{-2}$) | 957 | 22.7 | 12.7 | 10.4 | 72.6 |

¶Grand mean of the F1 segregating population across all six experiments.

### 3.6. *GGE biplot analysis*

GGE biplot analysis allows visual examination of the relationships among the test environments, genotypes, and the G×E interaction (Yan, 2000). As N is the key environmental variable affecting the important yield determining components of potato (Honeycutt et al., 1996), here we discuss only the results for trait NUE among the four experiments (Exps 3-4). The GGE biplots revealed that the 1st and the 2nd principal components accounted for 84.04% of the G×E variation (Fig. 3.5).

For any particular environment, genotypes can be compared by projecting a perpendicular from the genotype symbols to the environment vector, i.e. genotypes that are further along in the positive direction of the environment vector are better

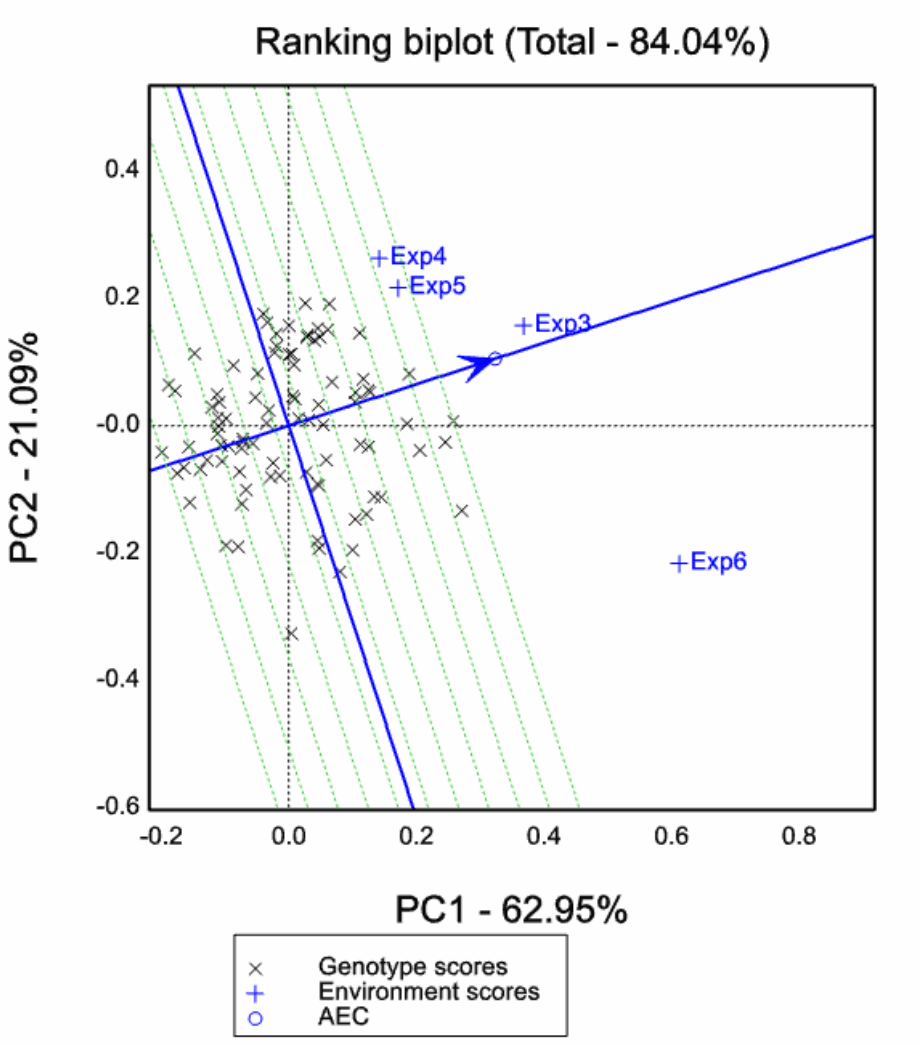


**Figure 3.5.** GGE biplot chart for nitrogen use efficiency (NUE) in an F1 segregating population. AEC indicates average environment coordinate (Yan, 2001; Yan and Kang, 2003). A line that passes through the biplot origin and average environment indicates the mean performance of genotypes.

performing and vice versa. The biplot chart indicated that genotypes performed exceptionally well in either low or high input environments (Fig. 3.5). This suggests that selection strategies can be developed for varieties with improved NUE. The results further showed that two environments (Exps 4 and 5) were grouped together. This suggests that these environments were highly correlated and relatively similar in the manner they discriminate among genotypes. The results further revealed that environments (Exps 4 and 5) fell close to the origin. This could mean that these environments might have little variability across genotypes (Kroonenberg, 1997). However, markers of environments (Exps 3 and 6) were standing furthest apart from the origin which might suggest that this environment caused maximum variability across the genotypes. These environments might therefore be the main contributor to the overall G×E on account of their lowest and high N availability, respectively (see Table 2.1 in Chapter 2) than the other environments.

### 3.7. *Estimates of broad-sense heritability*

All estimates of broad-sense heritability ($H^2$) (eqn (3.7)) were very high and they ranged from 80.2 to 96.8% (Table 3.5). In a previous section we showed that traits like $w_{max}$, RUE, and NUE were sensitive to environment. However, these traits also had very high heritability estimates, which could mean that they can respond to selection (Falconer and Mackay, 1996). High heritability estimates illustrate that these traits have a strong genetic basis, hence could be reliably assessed and used in breeding for resource (radiation, N) use efficiency as well as tuber dry matter production in potato.

### 3.8. *Phenotypic and genetic correlations of model parameters and the secondary traits*

Table 3.6 illustrates the phenotypic correlation coefficients among all the model parameters and secondary traits within the F1 segregating population across all six experiments. All phenotypic correlations were highly significant ($P$<0.01) (Table 3.6). The results showed strong negative phenotypic correlations between $c_m$ and $t_E$ ($r$ = -0.83) and between $c_m$ and $ED$ ($r$ = -0.84). These results suggest trade-off between tuber bulking rate and duration of tuber bulking. As mentioned earlier $t_B$ was stable, which means that $ED$ was almost exclusively determined by $t_E$; so, unsurprisingly there was a strong positive correlation between $t_E$ and $ED$. The results further revealed negative correlation ($r$ = -0.37) between RUE and NUE. This suggested a trade-off between RUE and NUE, mainly caused by their negative and positive

**Table 3.6.** Phenotypic (lower triangle) and genetic (upper triangle) correlation coefficients among all pair wise comparisons of different traits across six experiments of an F1 population of potato. *td* stands for thermal day.

| Parameter | $c_m$ | $t_E$ | *ED* | RUE | NUE | $w_{max}$ |
|---|---|---|---|---|---|---|
| $c_m$ (g $td^{-1}$) | – | -0.91** | -0.93** | 0.95** | -0.41** | -0.20** |
| $t_E$ (*td*) | -0.83** | – | 1.00** | -0.91** | 0.65** | 0.66** |
| *ED* (*td*) | -0.84** | 1.00** | – | -0.93** | 0.64** | 0.64** |
| RUE (g DM $MJ^{-1}$) | 0.69** | -0.65** | -0.65** | – | -0.75** | -0.25** |
| NUE (g DM $g^{-1}$ N) | -0.28** | 0.53** | 0.52** | -0.37** | – | 0.43** |
| $w_{max}$ (g $m^{-2}$) | -0.10** | 0.55 ** | 0.53 ** | -0.02 ** | 0.43** | – |

** Significant at 1%, NS Non-significant.

relationships with *ED*, respectively (Table 3.6).

There were weak but negative ($r$ = -0.10) phenotypic correlations between $c_m$ and $w_{max}$ (Table 3.6). However, the results indicated strong and positive phenotypic correlations between $t_E$, *ED*, and $w_{max}$ (i.e. $r$ = 0.55 and 0.53, respectively). From these results, it seems that both rate and duration of tuber bulking are of importance in determining final yield of potato crop. The positive role of NUE was evident from these results due to its positive phenotypic correlation with $w_{max}$ (i.e. $r$ = 0.43). This suggests that genotypes with high NUE may exhibit high tuber yield. The underlying relationships of $w_{max}$ with important traits are elaborately discussed in the next section.

Table 3.6 also illustrates the genetic correlation coefficients between the model parameters and secondary traits within the F1 population. The results of genetic correlations were in line with those of phenotypic correlations. As a whole the coefficient values for genetic correlations were comparatively higher than phenotypic correlations.

### 3.9. *Path coefficient analysis*

Table 3.7 presents the results of path coefficient analysis describing the direct and indirect effects of different traits on tuber dry matter yield ($w_{max}$), while Fig. 3.6 presents the path coefficient structural model describing important relationships among selected traits. The traits $A_{sum}$, RUE and $c_m$ had the highest direct effects on tuber dry matter yield ($w_{max}$) (Table 3.7). On the other hand, very low direct effects on $w_{max}$ were observed for traits *ED* and NUE (i.e. 0.06 and -0.04, respectively). The results further illustrated that higher value of direct effect of $A_{sum}$ on $w_{max}$ was the

**Table 3.7.** Path coefficient analysis of direct and indirect effects of different traits on the tuber dry yield ($w_{max}$) of an F1 population. *td* stands for thermal day.

| Variable | †Effect |
|---|---|
| $A_{sum}$ (*td* %) | |
| Direct effect | 1.34 |
| Indirect effect via | |
| $c_m$ | -0.20 |
| *ED* | 0.05 |
| RUE | -0.47 |
| NUE | -0.02 |
| ***Total correlation*** | **0.69** |
| $c_m$ (g $td^{-1}$) | |
| Direct effect | 0.32 |
| Indirect effect via | |
| $A_{sum}$ | -0.85 |
| *ED* | -0.05 |
| RUE | 0.47 |
| NUE | 0.01 |
| ***Total correlation*** | **-0.10** |
| *ED* (*td*) | |
| Direct effect | 0.06 |
| Indirect effect via | |
| $A_{sum}$ | 1.21 |
| $c_m$ | -0.27 |
| RUE | -0.46 |
| NUE | -0.02 |
| ***Total correlation*** | **0.53** |
| RUE (g DM $MJ^{-1}$) | |
| Direct effect | 0.69 |
| Indirect effect via | |
| $A_{sum}$ | -0.91 |
| $c_m$ | 0.22 |
| *ED* | -0.04 |
| NUE | 0.01 |
| ***Total correlation*** | **-0.02** |
| NUE (g DM $g^{-1}$ N) | |
| Direct effect | -0.04 |
| Indirect effect via | |
| $A_{sum}$ | 0.78 |
| $c_m$ | -0.09 |
| *ED* | 0.03 |
| RUE | -0.25 |
| ***Total correlation*** | **0.43** |

†Across six environments.

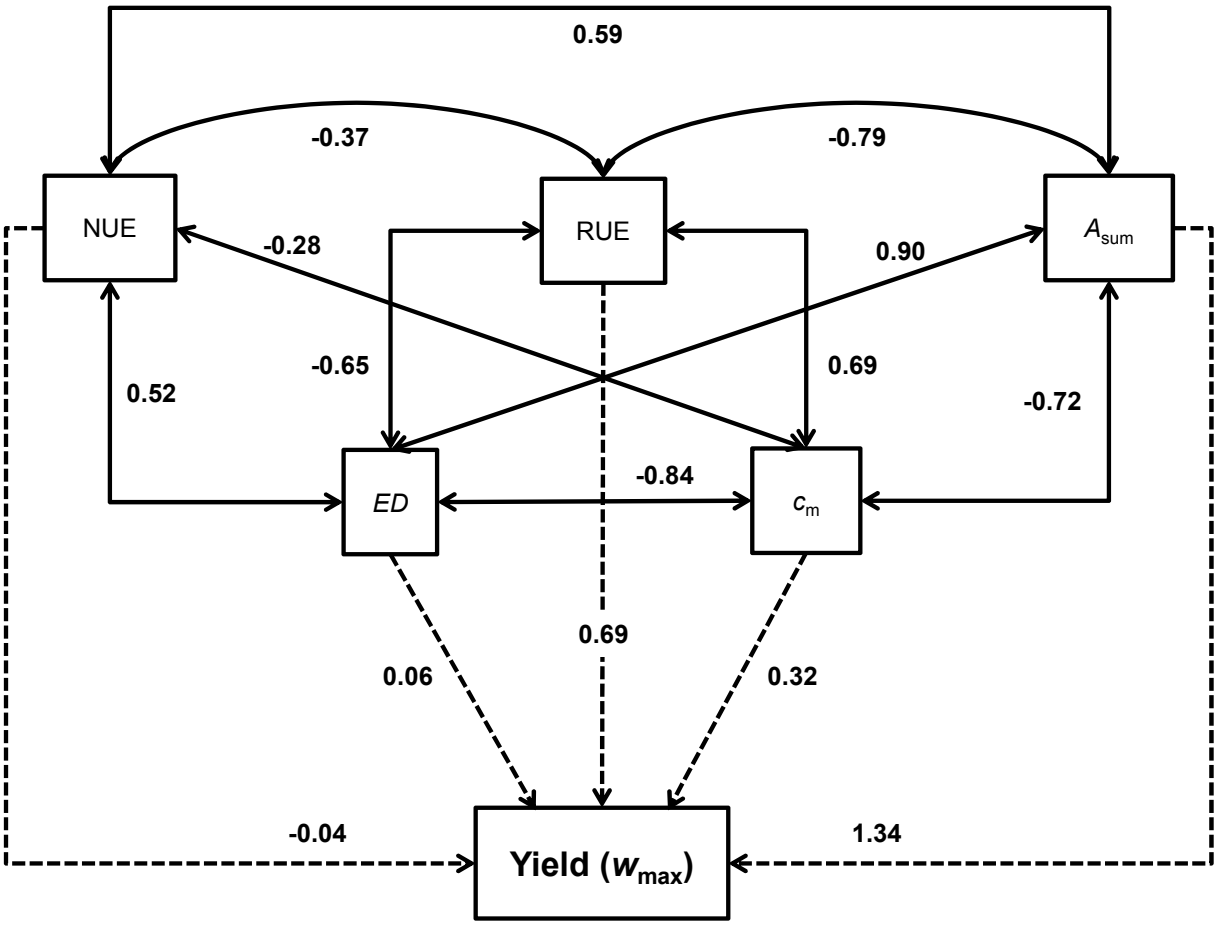


**Figure 3.6.** Path coefficient structural model describing direct and indirect effects of different traits on the tuber dry yield ($w_{max}$) across six experiments for an F1 segregating population of potato. The solid line represents the correlation coefficient between two predictor variables; dashed line represents the path coefficient from the predictor variable to response variable ($w_{max}$).

result of significant, strong positive correlation of $A_{sum}$ with *ED* ($r$ = 0.90) and NUE ($r$ = 0.59). On the other hand significant, strong, and positive correlations ($r$ = 0.80) between RUE and $c_m$ were reflected in their higher values of direct effect on $w_{max}$. Result further indicated that total correlation (i.e. sum of direct and indirect effects) between RUE and $w_{max}$ was only -0.02. This was mainly due to the strong negative indirect effect (-0.91) of $A_{sum}$ on RUE. The total correlation between $c_m$ and $w_{max}$ was also low (-0.10). In this case the strong indirect negative effect (-0.85) of $A_{sum}$ on $c_m$ also played its role.

The above results were further supported by the strong negative correlations between RUE and $A_{sum}$ ($r$ = -0.79) and $A_{sum}$ and $c_m$ ($r$ = -0.72) (Fig. 3.6). These suggested that genotypes with higher $A_{sum}$ exhibit slow tuber bulking rate in the

linear phase and may be less efficient in converting the radiation intercepted into dry matter yield of tubers. This could be related with the assimilation of dry matter and its distribution within the plant. Higher investment in terms of biomass allocation to vegetative organs may give high $A_{sum}$ and thereby higher total biomass, but on the other hand a relatively low proportion may be used for the production of tubers, especially if the maintenance requirements are high. Excessive vegetative growth can be compensated to only a limited extent by redistribution of dry matter from vegetative parts to tubers (Van Heemst, 1986).

Based on these results it can be strongly concluded that $A_{sum}$, RUE, and $c_m$ could be the traits having the strongest influence on the temporal dynamics of yield formation in potato. From a breeding perspective, an ideal genotype should have an optimal $A_{sum}$, without compromising RUE and $c_m$. Our path analysis between traits indicated the direction and magnitude of correlated responses to selection and the relative efficiency of indirect selection. In addition, our results suggest that while using these traits as a criterion for selection, other causal relationships must be considered simultaneously.

### 3.10. *QTL detection*

In total 16 QTLs were identified on both SH and RH parental genomes across all six environments. In the SH genome, three QTLs were associated with two linkage groups (I and V). Thirteen QTLs linked to seven linkage groups (IB, II, III, IV, V, VIII, and VIII) on the RH genome. Table 3.8 describes the number of QTLs detected per parental chromosome.

Table 3.9 summarises the list of QTLs detected, their parental chromosomes and map positions and their characteristics (i.e. additive effects and variance explained ($R^2$)) for each of the trait investigated for individual environment. All QTLs detected were significant at ($P$<0.05) with $-\log_{10}(P)$ values ranging from 3.52 to 67.99. The total fraction of phenotypic variance explained by effects of individual QTL ranged from <0.1% to 79%. The percentage of phenotypic variance was even higher when considering their global effects (ranging from 27% to 71%) (Table 3.9).

Three QTLs were detected for $c_m$ (Table 3.9). These QTLs were associated with linkage groups (RH V and RH VIII). Two QTLs were detected in Exps 1 and 3 with 63% and 35% associated combined QTL phenotypic variance, respectively. The other environments showed only one QTL. The major QTL 116_5_17 on linkage group RH V was commonly detected in most of environments. This QTL had maximum negative additive effect that ranged from 21.488 g $td^{-1}$ to 53.663 g $td^{-1}$ and explained 24% to 57% phenotypic variance. The other two additional QTLs (188_8_83 and 189_8_83)

**Table 3.8.** Distribution of QTLs detected on parental genomes.

| SH | | RH | |
|---|---|---|---|
| Linkage group | No. of QTLs | Linkage group | No. of QTLs |
| I | 2 | IB | 1 |
| V | 1 | II | 3 |
| | | III | 1 |
| | | IV | 1 |
| | | V | 4 |
| | | VIII | 2 |
| | | X | 1 |
| Total | 3 | | 13 |

on linkage group RH VIII had positive additive effects (i.e. 23.719 g $td^{-1}$ and 12.058 g $td^{-1}$) with 7% to 13% associated phenotypic variance, respectively.

Two QTLs were detected for $t_E$ and *ED* associated with two linkage groups (RH IB and RH V) (Table 3.9). One QTL was detected in all the environments a part from Exp 4 where two QTLs were detected. The phenotypic variance associated with combined QTLs detected in Exp 4 was about 70 %. QTL 116_5_17 on linkage group RH V was detected consistently in all the environments with associated phenotypic variance ranging from 62% to 79%. Here, this QTL had a maximum negative additive effect that ranged from -24.133 *td* to -66.019 *td*. The additional QTL 48_1_71 on linkage group RH IB had positive additive effects ranging from 9.561 *td* to 10.369 *td*. However, phenotypic variance explained by these additional QTLs was less than 1%.

In the case of RUE, at least one QTL was detected in most of environments apart from Exps 2 and 6, where two QTLs and no QTLs were detected, respectively (Table 3.9). The two QTLs found in Exp 2 jointly explained 47% of the phenotypic variance. The major QTL (116_5_17) on linkage group RH V was consistently found in environments with additive effects ranging from 0.641 g DM $MJ^{-1}$ to 1.732 g DM $MJ^{-1}$ with 24% to 55% associated phenotypic variance.

In total seven individual QTLs were detected for NUE (Table 3.9). The distribution of QTL s were such as three were found in Exp 3, two in Exps 5 and 6 and one in Exp 4 (Table 3.9). The phenotypic variance associated with multiple QTLs per environment ranged from 27% to 56%. Among the QTLs, 116_5_17 at position 18.2

**Table 3.9.** Main characteristics of quantitative trait loci (QTL) identified for different traits within the 'SH × RH' population per individual experiment (i.e. environment.). Data given in table are from the CIM mapping method. QTLs marked as bold are detected only by the CIM method, otherwise by both the CIM and SIM methods. Exp., experiment; position, position of maximum $-\log_{10}(P)$; a, additive effect of the presence of parental allele at a marker; $R^2$, the individual contribution of one QTL to the variation in a trait; global $R^2$, the fraction of the total variation explained by QTLs of the same trait within single environment ; *td*, thermal day. Symbols '–' and '*' mean lack of QTL and data, respectively.

| Parameter | Exp. | QTL | Linkage group | Marker name | Position (cM) | $-\log_{10}(P)$ | a | $R^2$ | Global $R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| $c_m$ (g $td^{-1}$) | 1 | 116_5_17 | RH V | EAGAMCTC_470_5_17 | 18.2 | 24.97 | 38.833 | 0.57 | 0.63 |
| | | **189_8_83** | **RH VIII** | **PAT/MAGG_149.8_8_83** | **74.5** | 3.62 | 12.058 | 0.07 | |
| | 2 | 116_5_17 | RH V | EAGAMCTC_470_5_17 | 18.2 | 22.93 | 53.663 | 0.56 | |
| | 3 | 116_5_17 | RH V | EAGAMCTC_470_5_17 | 18.2 | 6.84 | 35.736 | 0.24 | 0.35 |
| | | **188_8_83** | **RH VIII** | **PAG/MAGC_298.8_8_83** | **76.1** | 4.01 | 23.719 | 0.13 | |
| | 4 | 116_5_17 | RH V | EAGAMCTC_470_5_17 | 18.2 | 24.54 | 51.958 | 0.57 | |
| | 5 | 116_5_17 | RH V | EAGAMCTC_470_5_17 | 18.2 | 17.74 | 21.488 | 0.48 | |
| | 6 | 116_5_17 | RH V | EAGAMCTC_470_5_17 | 18.2 | 18.8 | 34.06 | 0.50 | |
| $t_E$ (*td*) | 1 | 116_5_17 | RH V | EAGAMCTC_470_5_17 | 18.2 | 67.62 | -55.624 | 0.79 | |
| | 2 | 116_5_17 | RH V | EAGAMCTC_470_5_17 | 18.2 | 36.78 | -54.458 | 0.68 | |
| | 3 | 116_5_17 | RH V | EAGAMCTC_470_5_17 | 18.2 | 19.376 | -38.459 | 0.63 | |
| | 4 | 116_5_17 | RH V | EAGAMCTC_470_5_17 | 18.2 | 34.7 | -38.968 | 0.65 | 0.70 |
| | | **48_1_71** | **RH IB** | **EACAMCGT_296.2_1_71** | **33.9** | 3.67 | 9.561 | <0.1 | |
| | 5 | 116_5_17 | RH V | EAGAMCTC_470_5_17 | 18.2 | 51.11 | -24.133 | 0.63 | |
| | 6 | 116_5_17 | RH V | EAGAMCTC_470_5_17 | 18.2 | 52.33 | -49.912 | 0.74 | |

**Table 3.9.** (Continued)

| Parameter | Exp. | QTL | Linkage group | Marker name | Position (cM) | -$\log_{10}(P)$ | a | $R^2$ | Global $R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| *ED* (*td*) | 1 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 67.99 | -60.873 | 0.79 | |
| | 2 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 37.54 | -60.247 | 0.68 | |
| | 3 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 18.756 | -41.077 | 0.62 | |
| | 4 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 36.23 | -43.013 | 0.66 | 0.71 |
| | | **48_1_71** | **RH IB** | **EACAMCGT_296.2__1_71** | **33.9** | 3.7 | 10.369 | <0.1 | |
| | 5 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 52.34 | -66.019 | 0.74 | |
| | 6 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 52.35 | -52.988 | 0.74 | |
| RUE | 1 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 22.72 | 1.732 | 0.55 | |
| (g DM $MJ^{-1}$) | 2 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 14.87 | 1.259 | 0.43 | 0.47 |
| | | 121_5_46 | RH V | EAACMCAG_231.8__5_46 | 52.6 | 6.74 | 0.402 | 0.15 | |
| | 3 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 9.862 | 1.329 | 0.39 | |
| | 4 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 16.32 | 1.135 | 0.45 | |
| | 5 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 6.67 | 0.641 | 0.24 | |
| | 6 | – | – | – | – | – | – | – | |

**Table 3.9.** (Continued)

| Parameter | Exp. | QTL | Linkage group | Marker name | Position (cM) | -$\log_{10}(P)$ | a | $R^2$ | Global $R^2$ |
|---|---|---|---|---|---|---|---|---|---|
| NUE | 1 | * | * | * | * | * | * | * | |
| (g DM $g^{-1}$ N) | 2 | * | * | * | * | * | * | * | |
| | 3 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 3.6 | -8.79 | 0.12 | 0.39 |
| | | 84_3_3 | RH III | PAT/MAAC_298.3__3_3 | 0 | 4.29 | 8.881 | 0.11 | |
| | | 204_10_34 | RH X | EAACMCCA_216.8__10_34 | 31.4 | 4.99 | -10.835 | 0.17 | |
| | 4 | 75_2_51 | RH II | EAGTMCAC_249__2_51 | 50.9 | 3.83 | -8.352 | 0.15 | |
| | 5 | **6_1_2** | **SH I** | **PAC/MACT_232.4__1_2** | **6.6** | 3.293 | -6.291 | 0.10 | 0.27 |
| | | 68_2_32 | RH II | PAT/MAAC_570.4__2_32 | 32.2 | 4.686 | -8.005 | 0.16 | |
| | 6 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 18.91 | -30.187 | 0.48 | 0.56 |
| | | **179_5_77** | **SH V** | **PAC/MATA_201.4__5_77** | **77.2** | 3.7 | 10.299 | 0.03 | |
| $w_{max}$ (g $m^{-2}$) | 1 | 117_5_37 | RH V | EACAMCGT_250.1__5_37 | 35.7 | 3.82 | 274.016 | 0.15 | |
| | 2 | 131_5_55 | RH V | PAC/MATA_99.4__5_55 | 62.6 | 4.36 | 246.053 | 0.18 | |
| | 3 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 15.84 | -630.531 | 0.44 | 0.53 |
| | | **81_2_75** | **RH II** | **PAC/MAGG_527.2__2_75** | **79.1** | 4.1 | -252.07 | 0.06 | |
| | 4 | 18_1_32 | SH I | EAACMCAG_187.9__1_32 | 36.3 | 3.52 | 244.584 | 0.13 | |
| | 5 | – | – | – | – | – | – | – | |
| | 6 | 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | 8.94 | -458.44 | 0.29 | 0.41 |
| | | **99_4_35** | **RH IV** | **EACAMCTG_69.5__4_35** | **11.2** | 4.46 | 256.493 | 0.08 | |

cM on the linkage group RH V was consistently detected in half of the environments explaining 12% to 48% phenotypic variance for NUE. This was a major QTL with its additive effects ranging from -8.79 g DM $g^{-1}$ N to -30.187 g DM $g^{-1}$ N in Exps 3 and 6, respectively. These results indicated a threefold decrease in additive effects of this QTL in the low N environment (i.e. Exp 3; see Table 2.1 in Chapter 2), which might suggest that alleles on paternal chromosome V at position 18.2 cM may reduce NUE less drastically under such low N conditions (Fig. 3.4). Moreover, four additional QTLs were detected on linkage groups (RH II, RH III, SH I and SH V) with their additive effects (-8.005, 8.881, -6.291, and 10.299 g DM $g^{-1}$ N, respectively). Interestingly, QTL 179_5_77 at position 77.2 cM on the maternal (SH) linkage group V was associated with a positive additive effect in Exp 6. This could suggest that alleles on the maternal and paternal linkage groups V are associated with negative and positive effects on NUE, respectively.

QTL mapping for tuber yield ($w_{max}$) *per se* showed six QTLs (Table 3.9). These QTLs were scattered over four parental linkage groups (SH I, RH II, RH IV, and RH V). The phenotypic variance explained by QTLs ranged from (6% to 44%). One QTL was detected in Exps 1, 2, and 4, whereas two QTLs were detected in Exps 3 and 6. No QTL could be detected in Exp 5. The multiple QTLs found in Exps 3 and 6 jointly explained 53% and 41% of the phenotypic variance, respectively. Among the total QTLs detected for this $w_{max}$, (116_5_17) on linkage group RH V was a major QTL detected in most of environments (i.e. Exps 3 and 6) with its additive effects ranging from -458.44 g $m^{-2}$ to -630.531 g $m^{-2}$ with 29% to 44% associated phenotypic variance, respectively (Table 3.9). These results are in line with NUE and suggest also that QTL (116_5_17) at position 18.2 cM on paternal linkage group V is sensitive to the environment particularly N as negative effects caused by alleles associated with this QTL changed in magnitude with respect to N availability. It is interesting to note that mean $w_{max}$ for Exp 3 was even higher than Exp 6 with high N availability (Table 3.3). As previously mentioned, variability among the genotypes was higher in Exp 3 for most traits (Fig. 3.4). It would be expected that the some genotype were most effective in this environment especially for NUE as suggested by the biplot analysis (Fig. 3.5). Therefore a focus on why particular genotypes perform exceptionally well in low or high input situations could enable selection strategies to be developed for improved varieties.

In order to summarise the QTL mapping results, QTLs with major effects were associated with paternal (RH) linkage group V, where maximum number of four QTLs was detected (Table 3.8 and 3.9). One particular QTL (i.e. 116_5_17) on paternal (RH) linkage group V at position 18.2 cM was detected for all traits with a major additive effect and explained most of the total phenotypic variance (Table 3.10). Additional

QTLs with minor effects was mostly associated with only paternal (RH) linkage groups for traits ($c_m$, $t_E$, and ED), whereas both maternal (SH) and paternal (RH) linkage groups were associated with traits NUE and $w_{max}$ for minor QTLs (Tables 3.9 and 3.10). Our results are in line with those by Van den Berg et al. (1996), who also reported that most of the QTLs had small effects, but a QTL with main effect was found on chromosome V. It was further noted that paternal QTL (116_5_17) was associated with its negative additive effects for most of the traits including tuber yield ($w_{max}$) *per se* except for $c_m$ and RUE, where this QTL showed the positive effects. This indicates that RH alleles for this QTL cause synergistic effects during the early phase of plant growth when the tuber bulking rates and RUE are at their maximum.

It was evident from our results that variation in tuber yield is associated with variation in bulking rate, duration of canopy cover, and associated extent of radiation interception (Fig. 3.6). However, these components are not physiologically independent as genotypes with a large tuber bulking rate may effectively limit the crop growth and duration (via enhanced internal plant competition) leading to their identified 'earliness'.

We also observed co-localisation of QTLs with many traits. For instance clustering of many QTLs were found on position 18.2 cM on paternal (RH) linkage group (Table 3.11). Here most of the traits (e.g. $c_m$, $t_E$, and *ED*) were tightly linked with QTL 116_5_17 in majority of the environments. This could mean that this QTL is playing a pleiotropic role in determining these traits. The strong genetic correlations between these traits confirm these relations (Table 3.6). This may indicate the difficulties of manipulating correlated traits simultaneously. However, QTLs with similar behaviours could also be interesting targets for breeding programmes as they are more likely to be stable under various environments. Our

**Table 3.10.** List of parental linkage groups with major and additional minor QTLs.

| Parameter | SH linkage group | RH linkage group | |
|---|---|---|---|
| | Minor QTLs | Major QTLs | Minor QTLs |
| $c_m$ | – | V | VIII |
| $t_E$ | – | V | IB |
| *ED* | – | V | IB |
| RUE | – | V | – |
| NUE | I, V | V | II, III, X |
| $w_{max}$ | I | V | II, IV |

results also indicated a number of independent QTLs mainly for NUE. These QTLs did not coincide with other traits (Table 3.12). These QTLs however, with minor effects could be of great value for breeding for NUE.

Several authors have indicated that some yield QTL coincide with those for component traits, whereas other yield QTL map independently from component traits (Xiao et al., 1995; Bezant et al., 1997). Few QTLs were expressed in one environment but not in the other (Table 3.13). This was mostly evident for traits RUE, NUE and $w_{max}$. The lower repeatability of some QTLs over the environments suggests QTL×E interaction. Our results support this as for these traits the environmental variance component contributed majorly to the total phenotypic variance for these traits (Table 3.4). QTLs controlling such traits often show low stability (Veldboom and Lee, 1996; Reymond et al., 2004). Several researchers have identified loci that interacted with the environment in different plant species e.g. yield in barley (Yin et al., 1999a,b; Teulat et al. 2001; Voltas et al., 2001).

Only one QTL 116_5_17 on RH V showed up in all the experiments (Table 3.14). This QTL was therefore stable across the environments and therefore did not show much of the QTL×E. Such QTLs could be useful for marker assisted breeding.

## 4. Conclusions

In this chapter we tried to elucidate the onset, rate, and duration of tuber bulking as yield-determining, complex quantitative traits in a set of varieties covering a wide range of maturity types and a well-adapted diploid F1 segregating population. We presented a physiological and quantitative genetic analysis of the traits underlying the dynamics of tuber bulking. Our model described well the tuber bulking dynamics and gave insight into the vital underlying component traits influencing the tuber dry matter production. Our results showed that tuber bulking growth rate ($c_m$) was comparatively higher for early maturing cultivars followed by late cultivars. However, the effective period of tuber bulking (*ED*) was longer for late maturing genotypes. As a result, tuber dry matter yield ($w_{max}$) was higher in late maturing genotypes than in mid-late and early genotypes.

We also studied resource (radiation and N) use efficiencies and their relationships with tuber dry matter yield production and with other important physiological traits. The RUE values were higher for early maturing genotypes followed by mid-late and late genotypes. Mean NUE values were higher for late maturing genotypes than for mid early and early cultivars. Late maturing cultivars have maximum canopy cover as well as a long tuber bulking period (*ED*) and therefore the highest tuber dry matter yields ($w_{max}$) per unit of N uptake.

**Table 3.11.** List of co-localised QTLs (i.e. QTLs were same for more than one trait).

| QTL | Linkage group | Marker name | Position (cM) | Exp. 1 | Exp. 2 | Exp. 3 | Exp. 4 | Exp. 5 | Exp. 6 |
|---|---|---|---|---|---|---|---|---|---|
| 48_1_71 | RH IB | EACAMCGT_296.2__1_71 | 33.9 | | | | $t_E$, *ED* | | |
| 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | $c_m$, $t_E$, *ED*, RUE | $c_m$, $t_E$, *ED*, RUE | $c_m$, $t_E$, RUE, NUE, $w_{max}$ | $c_m$, $t_E$, *ED*, RUE | $c_m$., $t_E$, *ED*, RUE | $c_m$, $t_E$, *ED*, NUE, $w_{max}$ |

**Table 3.12.** List of independent QTLs (i.e. QTLs detected only once for a particular trait in any environment).

| QTL | Linkage group | Marker name | Position (cM) | Exp. 1 | Exp. 2 | Exp. 3 | Exp. 4 | Exp. 5 | Exp. 6 |
|---|---|---|---|---|---|---|---|---|---|
| 6_1_2 | SH I | PAC/MACT_232.4__1_2 | 6.6 | | | | | NUE | |
| 18_1_32 | SH I | EAACMCAG_187.9__1_32 | 36.3 | | | | $w_{max}$ | | |
| 179_5_77 | SH V | PAC/MATA_201.4__5_77 | 77.2 | | | | | | NUE |
| 68_2_32 | RH II | PAT/MAAC_570.4__2_32 | 32.2 | | | | | NUE | |
| 75_2_51 | RH II | EAGTMCAC_249__2_51 | 50.9 | | | | NUE | | |
| 84_3_3 | RH III | PAT/MAAC_298.3__3_3 | 0 | | | NUE | | | |
| 99_4_35 | RH IV | EACAMCTG_69.5__4_35 | 11.2 | | | | | | $w_{max}$ |
| 117_5_37 | RH V | EACAMCGT_250.1__5_37 | 35.7 | $w_{max}$ | | | | | |
| 121_5_46 | RH V | EAACMCAG_231.8__5_46 | 52.6 | | RUE | | | | |
| 131_5_55 | RH V | PAC/MATA_99.4__5_55 | 62.6 | | $w_{max}$ | | | | |
| 189_8_83 | RH VIII | PAT/MAGG_149.8__8_83 | 74.5 | $c_m$ | | | | | |
| 188_8_83 | RH VIII | PAG/MAGC_298.8__8_83 | 76.1 | | | $c_m$ | | | |
| 204_10_34 | RH X | EAACMCCA_216.8__10_34 | 31.4 | | | NUE | | | |

**Table 3.13.** Number of QTLs detected across six experiments (environments). Symbols '–' and '*' mean lack of QTL and data, respectively.

| Parameter | Exp. 1 | Exp. 2 | Exp. 3 | Exp. 4 | Exp. 5 | Exp. 6 |
|---|---|---|---|---|---|---|
| $c_m$ | 2 | 1† | 2 | 1 | 1 | 1 |
| $t_E$ | 1† | 1 | 1 | 2 | 1 | 1 |
| *ED* | 1 | 1 | 1 | 2 | 1† | 1 |
| RUE | 1† | 2 | 1 | 1 | 1 | – |
| NUE | * | * | 3 | 1 | 2 | 2† |
| $w_{max}$ | 1 | 1 | 2† | 1 | – | 2 |
| Total QTLs | 6 | 6 | **10** | **8** | 6 | 7 |

† QTLs with maximum additive effects.

**Table 3.14.** List of stable QTLs across six experiments (i.e. Same QTLs detected in majority of environments).

| QTL | Group | Marker name | Position (cM) | Exp. 1 | Exp. 2 | Exp. 3 | Exp. 4 | Exp. 5 | Exp. 6 |
|---|---|---|---|---|---|---|---|---|---|
| 116_5_17 | RH V | EAGAMCTC_470__5_17 | 18.2 | × | × | × | × | × | × |

The prospects of improving a target trait by selecting for component traits are determined by the genetic variation for the particular component traits and their correlation with the target trait. High genetic variability along with high heritability was recorded for most of the traits. Phenotypic and genetic correlations were high ($r$ > 0.50) for these traits. The phenotypic and genetic correlations among model traits suggest a trade-off between $c_m$ and *ED* and between RUE and NUE. Path analysis showed that $c_m$, RUE, and $A_{sum}$ had a major influence on $w_{max}$.

The genetic parameters found in this study indicated existence of significant genetic variability within the F1 population for most traits studied. It was possible, therefore, to further analyse this wide genetic variability available, which could potentially be exploited in breeding programmes aimed at improving tuber bulking dynamics, RUE, NUE, and ultimately tuber dry matter production.

The AFLP markers were therefore used to perform QTL mapping of the model traits and resource (radiation, N) use efficiencies. In total 16 QTLs were identified on both SH and RH parental genomes across all six environments. QTLs with major

effects were associated mainly with paternal (RH) linkage group V. One particular QTL (116_5_17) on this linkage group was detected for nearly all the traits with a major additive effect and explained most of the total phenotypic variance. Additional minor QTLs were mostly associated with only paternal (RH) linkage groups for traits ($c_m$, $t_E$, and *ED*), whereas both maternal (SH) and paternal (RH) linkage groups were associated with traits NUE and $w_{max}$ for minor QTLs.

Our quantitative approach in combination with AFLP markers identified QTLs that could be useful in the development of marker assisted breeding strategies in potato yield improvement. It was evident from our results that variation in tuber yield is associated with variation in bulking rate, duration of canopy cover, and associated extent of radiation interception. However, these components are not physiologically independent as genotypes with a large tuber bulking rate may effectively limit the crop growth and duration (via enhanced internal plant competition) leading to their identified 'earliness'.

# CHAPTER 4

## Model-based evaluation of maturity type of potato using a diverse set of standard cultivars and a segregating diploid population*

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**Abstract**
The objective of this chapter is to evaluate the performance of the conventional system of classifying maturity type in potato and to provide a concept of maturity type based on crop physiology. We present an approach in which physiological traits are used to quantify and assess maturity type unambiguously for a set of varieties covering a wide range of maturity classes and a diploid F1 population separating for maturity and well-adapted to Dutch growing conditions, both grown in six environments. We defined physiological maturity based on four traits: the duration of maximum green canopy, the area under the green canopy cover progress curve, and the rate and duration of tuber bulking. The results indicated that physiological maturity type criteria tended to define maturity classes less ambiguously than the conventional criterion. Moreover, the conventional criterion was subject to more random noise and lacked stability and/or repeatability compared with the physiological traits. The physiological maturity criteria also illustrated the physiological trade-offs that existed between the selected traits and underlined the subtle complexities in classifying maturity type. This study highlighted the capabilities of different maturity type criteria in discriminating between different maturity classes among the large set of genotypes. Our new approach involving key physiological traits could be beneficial in offering physiology-based criteria to re-define maturity type. An improved criterion based on important physiological traits would allow relating the maturity to crop phenology and physiology. This new criterion may be amenable to further genetic analysis and could help in designing strategies for potato ideotype breeding for genotypes with specific maturity types.

**Key words:** Potato (*Solanum tuberosum* L.), tuber bulking, earliness, maturity type, breeding, segregating population, cultivar choice, statistical tools.

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## 1. Introduction

Crops undergo sequential developmental phases from emergence to senescence that are characterised by their chronological age, but also by their phenology and reproductive capacity. In most annual crop plants, the transition from the vegetative to the reproductive phase is marked by the onset of flowering and seed production; hence fully reproductive plants are considered mature (Bond, 2000). However, in the case of potato (*Solanum tuberosum* L.), most genotypes maintain the capacity to develop new leaves and continue to grow throughout the major part of their life cycle thanks to the fact that at least some vegetative meristems remain indeterminate (Vos and Biemond, 1992; Struik and Ewing, 1995; Vos, 1995a; Almekinders and Struik, 1996; Fleisher et al., 2006). Progress to maturity is therefore difficult to assess in potato.

Crop development in potato is a complex trait that may be comprised of a series of phenological events such as completion of canopy growth, termination of sympodial growth, the onset of tuber formation, or the onset of the rapid increase in harvest index, sagging of plants, senescence of leaves, etc. (Struik et al., 2005; Struik, 2010). The sequential phases of growth determining the duration of phenological stages of potato genotypes could be used to understand and define the concept of maturity type and to clearly classify genotypes.

The conventionally used definition of maturity type in potato, however, is rather ambiguous (Haga et al., 2012). Many public and private institutions have tried to define the maturity in potato and have come up with their own definitions. Public institutions such as the International Union for the Protection of New Varieties of Plants (UPOV), and the authorities involved in granting plant breeders' rights use foliage maturity as descriptor among the many traits for DUS (Distinct, Uniform, Stable) criteria. Maturity (Trait 36) in the UPOV document (http://www.upov.int/edocs/tgdocs/en/tg023.pdf) is using the criterion "*The time of maturity is reached when 80% of the leaves are dead*." Private institutions, such as breeding companies and marketing boards release brochures to advertise the specificities of their cultivars. Maturity type indications in these brochures are usually based on the personal scale of the breeder. Furthermore, several databases on the World Wide Web are available such as "the European cultivated potato database", (http://europotato.org/display_character.php?char_no=18&character=Maturity).

It is remarkable, that many seem to know how to classify plants into a specific scale, and even to make conversion from one scale to another, without a proper definition of this complex syndrome of developmental events. As a whole, the conventional method or criterion of elucidating the maturity type used is mostly based on visual observations made in the field at particular time intervals during the

crop cycle and transferring that information to unit-less ordinal scales. This criterion does not have any biological meaning and involves ambiguity and much speculation in understanding the background of maturity, partly because of the different viewpoints of growers and processors. For instance, the grower may consider maturity as the onset of canopy senescence and/or when there is no further net growth (Bodlaender and Reestman, 1968). The processor on the other hand may consider the declining levels of reducing sugars in the tubers as an indication of approaching maturity (Burton and Wilson, 1970). Yet others think maturity to be synonymous with tuber dry matter concentration (Beukema and van der Zaag, 1979).

On account of such discrepancies, the conventional maturity criterion may also not be stable (changes of the maturity class of a particular variety have often been reported), subject to personal bias and showing strong genotype-by-environment (G×E) interaction. Hence, there is a strong need for a clear and unambiguous definition of the maturity type of potato genotypes based on a clear understanding of potato physiology and of the G×E. Crop physiologists, agronomists and breeders would all profit from such a clear definition. Studies by Struik et al. (2005) and Struik (2010) have shown that redefining the potato maturity based on physiological traits is promising.

Current state of the art in statistical knowledge and techniques has made it possible to properly analyse large amounts of available physiological and genetic information. For instance, cluster analysis and path coefficient analysis are useful in explorative data mining, information retrieval, and data summarisation. Cluster analysis offers a meaningful grouping and/or sub-grouping based on similarities found in the data. Additionally, it offers ways to characterise each group in terms of a cluster prototype, i.e. a data object that is representative of the other objects in the group. This may help in pattern recognition, targeting appropriate treatment(s), and studying typologies as well as finding the genetic relationships and/or diversity among the large set of genotypes (Dunemann et al., 1994; Piluzza et al., 2005; Arshad et al., 2006; Ram et al., 2008). In addition, procedures like path coefficient analysis has proven to be useful in giving thorough understanding of relationships and contribution of various characters to the target trait by partitioning the correlation coefficient into components of direct and indirect effects. Bhatt (1972) reported that merely correlation studies do not clearly reveal such type of information and can be misleading if the high correlation between two traits is a consequence of the indirect effect of the traits (Dewey and Lu, 1959).

Given the rich quantitative data set at hand from Chapters 2 and 3 and the availability of state of the art statistical tools, this chapter aims to evaluate, quantify, and re-define the concept of maturity type of a large set and diverse set of genotypes

of potato. Our objective is to develop a physiological approach of assessing maturity type during the whole course of plant development. This method should be reliable, robust and should allow the phenotyping of large numbers of genotypes across diverse environments. This study will also provide more insight into the genetic–physiological linkage of maturity type in potato.

## 2. Materials and methods

### 2.1. Set-up of experiments

Data sets for our analysis came from six field experiments, performed in Wageningen (52° N latitude), the Netherlands, during 2002, 2004, and 2005 with two experiments in each year. These experiments differed in environmental conditions because they were carried out in different years, on different soils, and under different N fertiliser regimes (for details, see Chapter 2). The experiments were conducted under stress-free growing conditions and the statistical designs used were randomized complete block designs with two blocks. The planting material consisted of disease-free, uniform sized seed tubers of similar physiological quality from an F1 diploid ($2n=2x=24$) potato population (100 genotypes) derived from a cross between two diploid heterozygous potato clones, SH83-92-488 × RH89-039-16, or simply the 'SH×RH population' (Rouppe van der Voort et al., 1997; Van Os et al., 2006). This population segregates for maturity type and is well-adapted to Dutch conditions (Van der Wal et al., 1978; Van Oijen, 1991) thus making it ideal for this study. A set of five standard cultivars (viz. Première, Bintje, Seresta, Astarte, and Karnico) covering a wide range of maturity types under Dutch conditions were also included in this study to bench mark the effects of maturity type among known genotypes.

### 2.2. Analytical approach

#### 2.2.1. *Selection of physiological traits*

Maturity is a complex phenomenon affected by many components of crop growth and development. However, the variation in maturity between the genotypes could be reflected in differing periods of attaining critical physiological stages such as canopy development, tuber initiation, filling, and their total duration. In Chapters 2 and 3, we developed physiological approaches to quantify the dynamics of canopy development

and of tuber bulking of potato during the entire crop cycle in the aforementioned large set of genotypes. This work yielded a large set of biologically meaningful and genetically relevant component traits directly related to the ability of the genotypes to intercept photosynthetically active radiation and tuber dry matter production. Most of these traits successfully explained part of the genetic variation in maturity type and could be used to enhance the breeding efforts aiming at elucidating potato maturity. In this study, however, for the sake of simplicity, we selected only four traits: $D_{P2}$, $c_m$, $ED$, and $A_{sum}$ based on their strong genetic nature and very high response to direct selection (Chapter 6). $D_{P2}$ is the duration of the phase with maximum and constant canopy cover (in thermal days (*td*)). $A_{sum}$ is the area under whole green canopy cover curve (in *td* %), $c_m$ is the rate of tuber bulking (in g $m^{-2}$ $td^{-1}$) and $ED$ is the duration of tuber bulking (in *td*).

### 2.2.2. *Criteria for re-defining genotype maturity type*

In the Netherlands, according to the conventional system, potato varieties are officially classified into four main maturity classes: very early, early/mid-early, mid-late/late, and very late. However, for the sake of simplicity maturity classes early/mid-early and mid-late/late were considered as early and late, respectively, throughout the text, tables, and figures. Genotypes were allocated to maturity classes (very early, early, late, and very late) based on each of the four selected physiological trait using the Ward's minimum-variance clustering method in SAS software (SAS Institute Inc. 2004). A schematic representation of cluster analysis for identifying different maturity classes is described by Fig. 4.1. The input data consisted of means of F1 genotypes, their two parents, and five standard cultivars across six environments.

After the identification of the maturity classes, further sub-clustering of genotypes within each maturity class was done using the nearest neighbour clustering method. Each sub-cluster of genotypes within each of the maturity classes was assigned different maturity scores according to the Netherlands Potato Consultative Foundation (NIVAP, 2007), for instance, maturity scores 8.0, 8.5, 9.0 and 9.5 in the cluster of very early genotypes, maturity scores 2.0, 2.5, 3.0, 3.5 for very late, etc. Table 4.1 describes the ranges of scales for each maturity type. Finally, this whole procedure resulted into re-defined maturity type criteria based on our four selected physiological traits. The scoring procedure was employed in order to make later comparison possible between the conventional and newly re-defined criteria of genotype maturity type, now referred to as "physiological maturity type criteria" throughout the remaining text. For the conventional criterion, we followed the

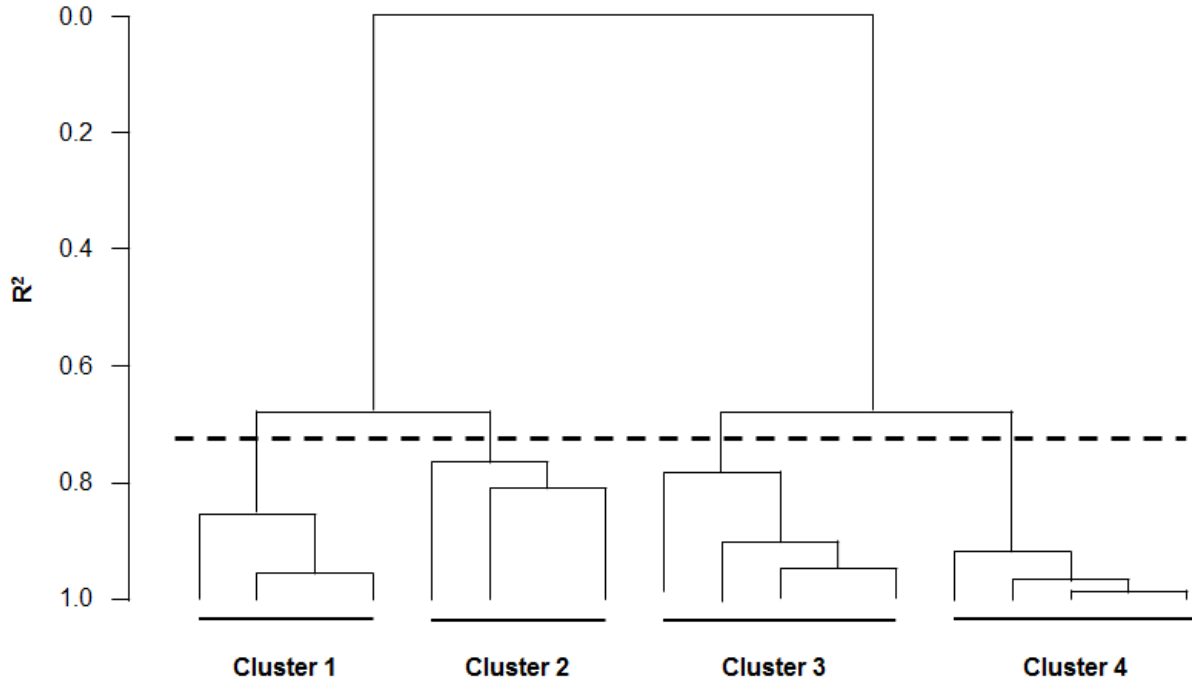


**Figure 4.1.** A schematic representation of cluster analysis for single trait x within F1 population, where x = $D_{P2}$ or $c_m$ or $ED$ or $A_{sum}$. The dashed line shows hypothetical intersection of four main clusters for the selection of four maturity classes (very early, early, late, and very late).

general practice used by breeders, i.e. visual observations were made in the field at particular time intervals during the crop cycle and the information was transferred to unit-less ordinal scales. For the F1 population we had the breeders' assessments (i.e. genotype maturity scales) based on two experiments (environments) during 2002.

**Table 4.1.** List of ordinal scale values for different maturity classes.

| Maturity class | Type | Scale values |
|---|---|---|
| 1 | Very early | 8.0, 8.5, 9.0, 9.5 |
| 2 | Early | 6.0, 6.5, 7.0, 7.5 |
| 3 | Late | 4.0, 4.5, 5.0, 5.5 |
| 4 | Very late | 2.0, 2.5, 3.0, 3.5 |

### 2.3. Statistical analysis

All statistical analyses were carried out using Genstat computer software (Payne et al., 2009). Path coefficient analysis was performed to ascertain the inter-associations between our selected physiological traits following the approach of Dewey and Lu (1959). The non-parametric Mann-Whitney U test was used to check the significance of differences between the conventional and physiological maturity criteria for the F1 population. Descriptive statistics was performed and the relationships between maturity scores per maturity criterion (i.e. conventional and re-defined criteria) were assessed using the Pearson correlation coefficient. Finally, regression analysis was performed to check the capability of conventional and physiological maturity criteria to predict the maturity type of genotypes. As data consisted of ordinal scales, data was log-transformed prior performing the correlation and regression analysis to satisfy test assumptions.

## 3. Results and discussion

### 3.1. Path coefficient analysis

We surmised based on our previous results (see Chapters 2 and 3) that $A_{sum}$ could be seen as an expression of a series of underlying physiological, genetic, and environmental processes and interactions affecting the maturity and yield production in potato (cf. Vos, 1995b; 2009). Path coefficient analysis was therefore accomplished by partitioning the direct and indirect effects of our selected physiological traits upon $A_{sum}$. Figure 4.2 presents the path coefficient structural model describing important relationships among selected physiological traits. Among the selected traits, *ED* and $D_{P2}$ had the highest direct effects on $A_{sum}$ (0.69 and 0.51, respectively, see dashed lines in Fig. 4.2). On the other hand, $c_m$ showed the lowest (0.22) direct effect on $A_{sum}$. The results further indicated a strong positive correlation between $D_{P2}$ and *ED* ($r$ = 0.79) and negative correlations between $c_m$ and $D_{P2}$ ($r$ = -0.63); $c_m$ and *ED* ($r$ = -0.93) (Fig. 4.2). These results suggest that genotypes with higher tuber bulking rates ($c_m$) exhibit lower $D_{P2}$ or *ED* and may mature early. Compared with late genotypes, early genotypes allocate a large part of their available assimilates to the tubers early in the growing season, leading to shorter crop cycle (Kooman and Rabbinge, 1996). In conclusion, path coefficient analysis indicated that progress to maturity in potato is strongly influenced by our selected physiological traits. Based on the strength of their direct effects on crop maturity, such traits could be categorised in following order:
$ED > D_{P2} > c_m$.

### 3.2. Descriptive analysis of different maturity type defining criteria

The first step in the analysis was to apply some standard descriptive statistical methods to the data. Table 4.2 shows the means, standard deviations, and minimum, maximum values of genotypes allocated in maturity classes under conventional and

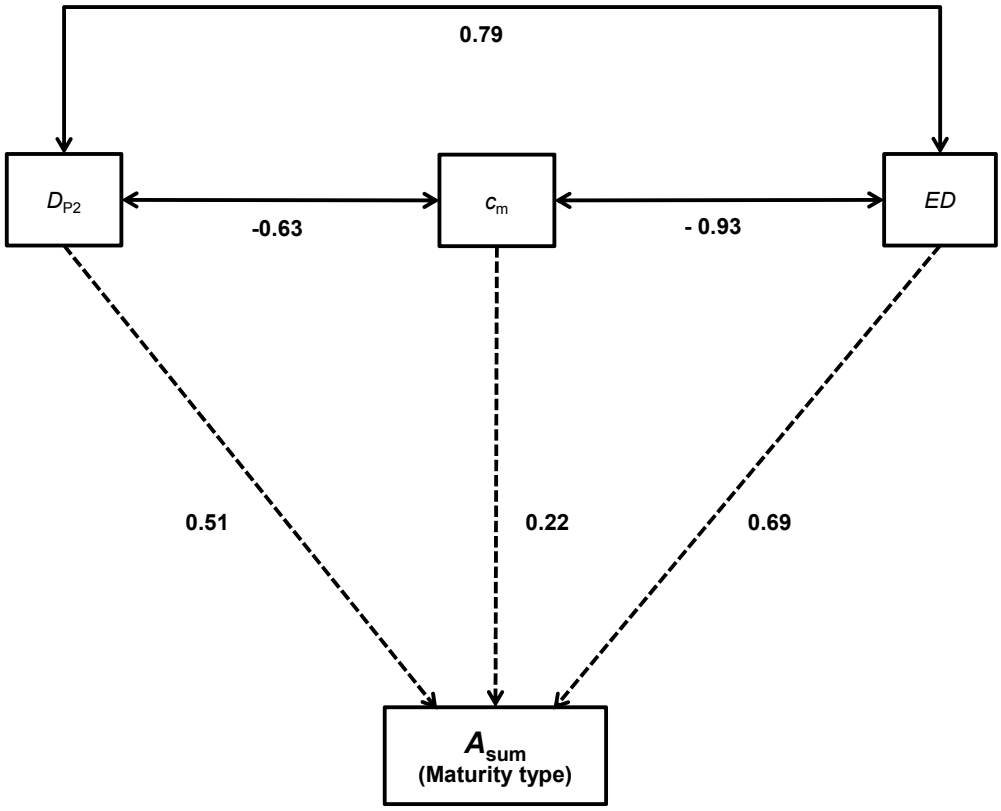


**Figure 4.2.** Path coefficient structural model describing direct and indirect effects of different traits on the maturity type (defined by $A_{sum}$ i.e. area under whole green canopy curve) across six experiments in an F1 population. $D_{P2}$ represents the duration of maximum green canopy phase, $c_m$ and *ED* are growth rate and effective duration of the linear phase of tuber bulking, respectively. The solid line represents the correlation coefficient between two predictor variables; dashed line represents the path coefficient from the predictor variable to response variable ($A_{sum}$). See Materials and Methods for further details.

**Table 4.2.** Mean, minimum (Min), maximum (Max) values of maturity scores, and percentage (%) of genotypes allocated to each maturity class for five different maturity type criteria within the F1 population (100 genotypes).

| Maturity type criterion[1] and class | Mean (±S.E.)[2] | Min | Max | % |
|---|---|---|---|---|
| ***Conventional*** | | | | |
| Very early | 8.3 (±0.1) | 8.0 | 9.5 | 35.4 |
| Early | 7.0 (±0.1) | 6.0 | 7.5 | 53.8 |
| Late | 4.9 (±0.1) | 4.5 | 5.5 | 8.6 |
| Very late | 3.0 (±0.5) | 2.5 | 3.5 | 2.2 |
| $\boldsymbol{D_{P2}}$ | | | | |
| Very early | 8.3 (±0.2) | 8.0 | 9.0 | 7.3 |
| Early | 6.9 (±0.1) | 6.0 | 7.5 | 69.7 |
| Late | 4.8 (±0.1) | 4.0 | 5.5 | 16.5 |
| Very late | 2.8 (±0.2) | 2.0 | 3.5 | 6.4 |
| $\boldsymbol{c_m}$ | | | | |
| Very early | 8.6 (±0.1) | 8.0 | 9.5 | 18.5 |
| Early | 6.5 (±0.1) | 6.0 | 7.5 | 33.3 |
| Late | 4.9 (±0.1) | 4.0 | 5.5 | 34.3 |
| Very late | 2.9 (±0.1) | 2.0 | 3.5 | 13.9 |
| ***ED*** | | | | |
| Very early | 8.7 (±0.1) | 8.0 | 9.5 | 52.8 |
| Early | 7.1 (±0.1) | 6.0 | 7.5 | 16.7 |
| Late | 4.6 (±0.2) | 4.0 | 5.5 | 10.2 |
| Very late | 2.7 (±0.1) | 2.0 | 3.5 | 20.4 |
| $\boldsymbol{A_{sum}}$ | | | | |
| Very early | 8.8 (±0.2) | 8.0 | 9.5 | 7.3 |
| Early | 7.0 (±0.1) | 6.0 | 7.5 | 62.4 |
| Late | 4.8 (±0.1) | 4.0 | 5.5 | 23.9 |
| Very late | 2.9 (±0.2) | 2.0 | 3.5 | 6.4 |

[1] Conventional scale: based on breeders' criteria; $D_{P2}$ scale: based on duration of maximum green canopy cover; $c_m$ scale: based on tuber bulking rate; *ED* scale: based on effective duration of linear tuber bulking; $A_{sum}$ scale: based on the area under whole green the canopy curve.

[2] Mean of F1 segregating population (100 genotypes) across six environments.

physiological maturity type criteria. The mean values of maturity scaling varied significantly ($P$<0.01) across four maturity classes (very early, early, late, and very late) for each maturity type criterion. Examination of the minimum and maximum values illustrated that mean ranges of maturity classes were consistently similar between different maturity type criteria. This was a kind of check and proved that our procedure of assigning the maturity scores was satisfactory. However, the percentage of genotypes allocated to each maturity class differed among maturity type criteria (Table 4.2). For maturity class 'very early', the $D_{P2}$ and $A_{sum}$ maturity type criteria allocated minimum (7.3%) of total genotypes, while the *ED* criterion allocated the maximum (52.8%) number of genotypes. In case of maturity class 'early', the *ED* and $D_{P2}$ criteria allocated the minimum (16.7%) and maximum (69.7%) of total genotypes, respectively. For 'late' maturity class, the conventional criterion allocated the minimum (8.6%) whereas the criterion based on $c_m$ allocated the maximum (34.3%) of total genotypes. On the other hand, minimum (2.2%) and maximum (20.4%) of total genotypes were allocated to maturity class 'very late' by the conventional and *ED* maturity–type criteria, respectively.

These results illustrated the capabilities of these different maturity type defining criteria in describing the extent of maturity type among the large set of unknown genotypes.

### 3.3. Comparison of different maturity type criteria

The statistical comparison of different maturity type criteria for the F1 population is presented in Table 4.3. Results of the non-parametric Mann-Whitney U test showed that there were significant ($P$<0.01) differences in maturity scores among the five criteria except between conventional and *ED* and between $D_{P2}$ and $A_{sum}$ (Table 4.3).

Figure 4.3 evaluates differences in maturity scales for standard cultivars. All maturity criteria gave different scales to the standard cultivars. More or less similar trend of maturity scaling was observed across the criteria following the order: Première > Bintje > Seresta > Astarte > Karnico (Fig. 4.3).

The results indicated furthermore that Première was marked as 'very early' by most of the criteria. However, according to $D_{P2}$ and $A_{sum}$ criteria, Première was placed in the 'early' category. Bintje was marked as 'early' by all criteria, except the $c_m$ criterion which put Bintje in the 'very early' category. Cultivar Seresta was marked as 'late' by the conventional, $c_m$ and *ED* criteria, but the same cultivar was considered 'very late' by $D_{P2}$ and $A_{sum}$ criteria. Astarte and Karnico were marked as 'very late' by all criteria except $c_m$ which considered these cultivars 'late'. Apparently $c_m$ and conventional criterion showed least and maximum resolution, respectively for maturity type among the standard cultivars.

**Table 4.3.** Mann-Whitney U test for checking extent of variation among different maturity type criteria.

| Maturity class[1] | Mann-Whitney U test[2] |
|---|---|
| *Conventional scale versus* | |
| $D_{P2}$ scale | ** |
| $c_m$ scale | ** |
| *ED* scale | NS |
| $A_{sum}$ scale | ** |
| | |
| $D_{P2}$ *scale versus* | |
| $c_m$ scale | ** |
| *ED* scale | ** |
| $A_{sum}$ scale | NS |
| | |
| $c_m$ *scale versus* | |
| *ED* scale | ** |
| $A_{sum}$ scale | ** |
| | |
| *ED scale versus* | |
| $A_{sum}$ scale | ** |

[1] Conventional scale: based on breeders' criteria; $D_{P2}$ scale: based on duration of maximum green canopy cover; $c_m$ scale: based on tuber bulking rate; *ED* scale: based on effective duration of linear tuber bulking; $A_{sum}$ scale: based on the area under the whole green canopy progress curve.

[2] ** Significant at 1%, NS= non-significant.

These results highlighted the complexities in defining the maturity type in potato. It was notable that although conventional maturity criterion was able to classify the genotypes into different maturity classes, it could not offer a clear definition. In contrast, results from physiological maturity type criteria were easily and clearly interpretable. Our integrated approach involving different physiological traits therefore could be very beneficial in offering physiology-based criteria to re-define maturity type.

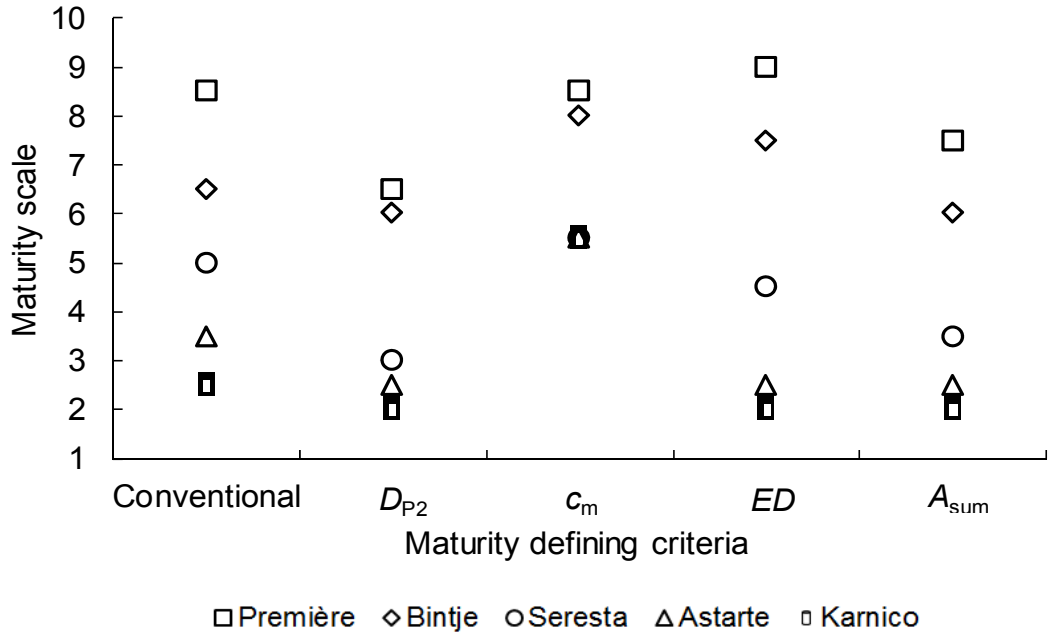


**Figure 4.3.** Comparison of conventional and physiological maturity type criteria for five standard cultivars. $D_{P2}$ represents the duration of maximum green canopy phase, $c_m$ and *ED* are growth rate and effective duration of the linear phase of tuber bulking, respectively, $A_{sum}$ is area under whole green canopy curve.

### 3.4. Performance and stability of conventional maturity type criterion

Our next objective was to check the performance of the conventional criterion in terms of its capacity to clearly pick up genotypes for each physiological trait (i.e. $D_{P2}$, $c_m$, *ED*, and $A_{sum}$). Considerable overlapping among the maturity classes was observed in the conventional criterion (Fig. 4.4). The extent of stability and/or repeatability of maturity scores from the conventional criterion were checked for the quantitative physiological traits.

Figure 4.5 compares the maturity scores from conventional method for one physiological trait $A_{sum}$. The results indicated that $A_{sum}$ values showed a lot of variation both within and throughout different maturity classes. For instance, it was noted that the conventional criterion could not identify genotypes with high $A_{sum}$ (i.e. very late genotypes) as evident from the lack of maturity scores in the range of 2-4 (Fig. 4.5).

These results indicated the weakness and lack of robustness of conventional maturity criterion in dealing with rather complex physiological quantitative traits. It can be concluded that such criterion is not quite able to clearly interpret and discriminate between maturity classes for the crucial growth related processes of

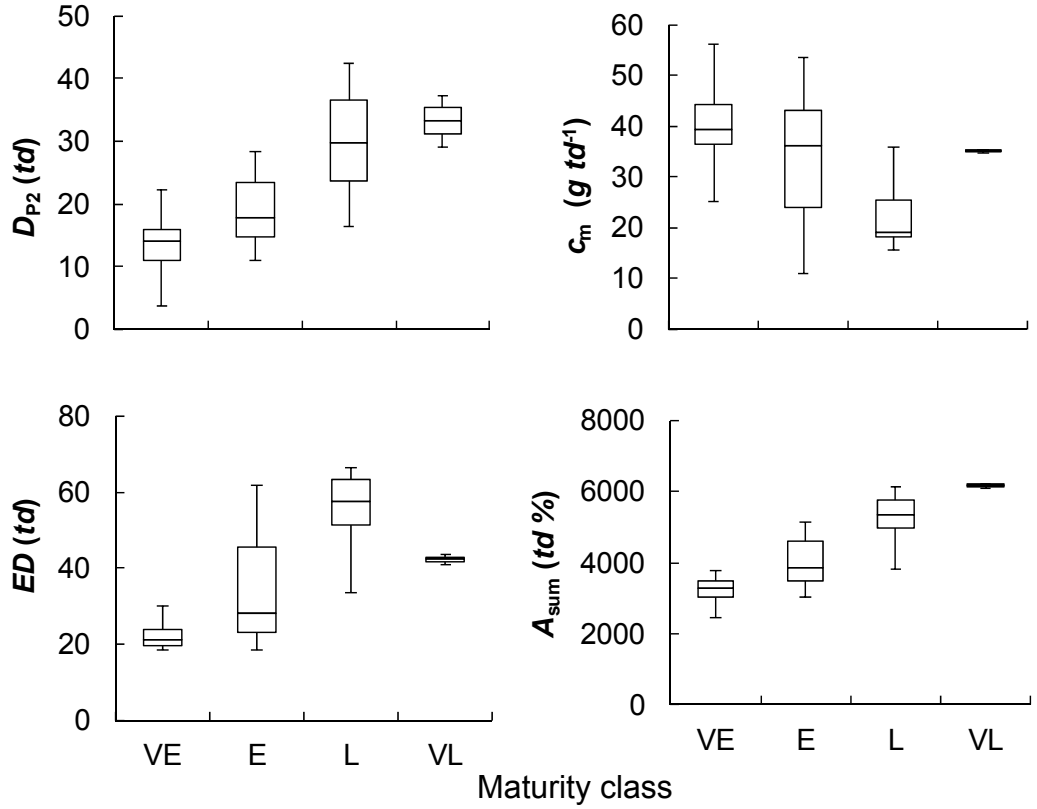


**Figure 4.4.** Box plots illustrating the ranges of genotypes in four maturity classes as assessed by conventional criterion for physiological traits: $D_{P2}$, $c_m$, *ED*, and $A_{sum}$, within the F1 population (100 genotypes). $D_{P2}$ represents the duration of maximum green canopy phase, $c_m$ and *ED* are growth rate and effective duration of the linear phase of tuber bulking, respectively and $A_{sum}$ is area under whole green canopy curve. The boxes span the interquartile range of the trait values, so that the middle 50% of the data lay within the box, with a horizontal line indicating the median. Whiskers extend beyond the ends of the box as far as the minimum and maximum values. VE= very early; E=early; L=late; VL=very late.

potato. An improved criterion based on important physiological traits would allow relating the maturity to crop phenology and physiology. Haga et al. (2012) used flower development, leaf chlorophyll content and leaf peroxidase activity to classify maturity of potato cultivars under temperate conditions. They observed that leaf chlorophyll content was the most reliable indicator among these three variables, an indicator related to $A_{sum}$ as both reflect leaf senescence. However, leaf chlorophyll content was mainly capable of discriminating between late and early-medium or medium-late; it did not separate early-medium from medium-late cultivars well.

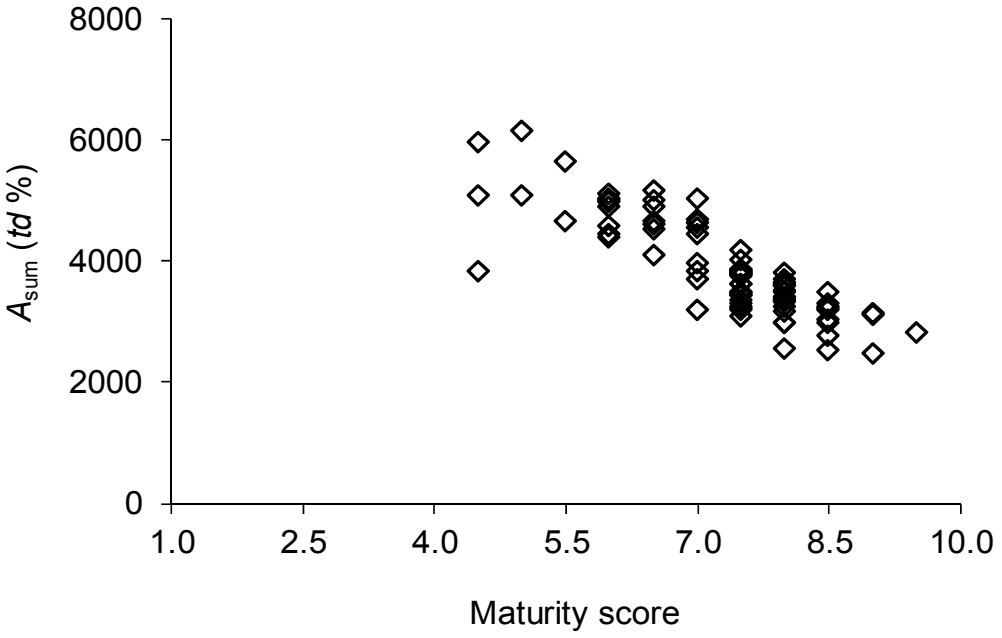


**Figure 4.5.** Extent of stability and/or repeatability of maturity scores from a conventional criterion for quantitative traits, for instance $A_{sum}$ (i.e. area under whole green canopy cover curve) within the F1 population.

Our physiological based criteria of defining the maturity type could allow in clear discriminating between all classes.

### 3.5. Predictive capability of different maturity type criteria

Different maturity criteria were analysed for their capabilities to predict the maturity in a large number of unknown genotypes across diverse environments. The regression analysis was performed on the maturity scores from each maturity criterion. So far our results indicated that nearly all physiological traits satisfactorily defined the maturity type. However, for the sake of simplicity, here we consider only one trait $A_{sum}$ as a synonym to the response variable "maturity". Figure 4.6 shows the results of regression between the observed $A_{sum}$ and the $A_{sum}$ ("maturity type") as predicted by regression analysis from the individual maturity criteria. The results indicated that almost all maturity criteria predicted the maturity well, i.e. $R^2 > 0.50$. However, the conventional and $c_m$ based criteria predicted the maturity comparatively less accurately with $R^2$ values 0.68 and 0.51, respectively. Maturity criterion based on *ED* gave the best ($R^2 = 0.81$) predictions for maturity type followed

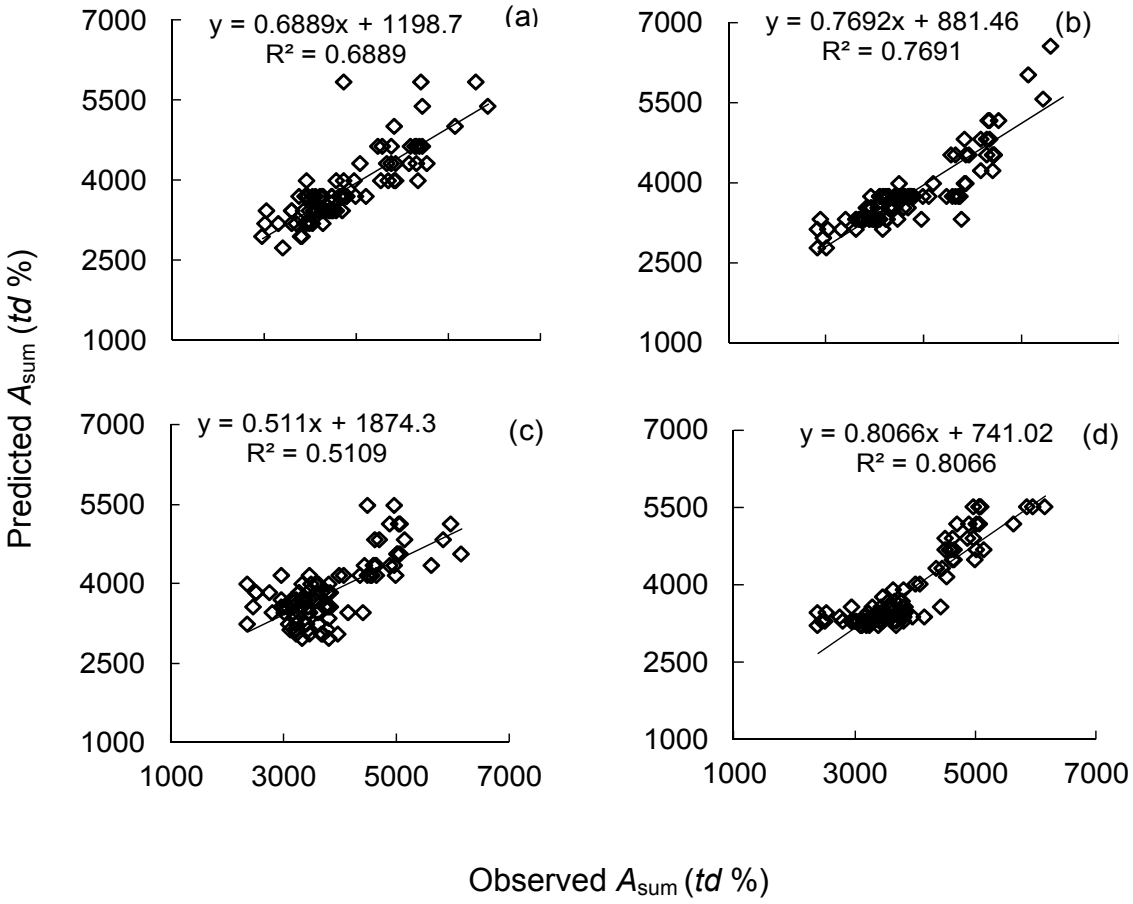


**Figure 4.6.** Comparison of different maturity type criteria for predicting the $A_{sum}$ (as a proxy for maturity type) within the F1 population across six environments. Panels show regression analysis based on different maturity type criteria, i.e. (a) conventional, (b) $D_{P2}$ (duration of maximum green canopy phase), (c) $c_m$ (growth rate during linear phase of tuber bulking), (d) *ED* (effective duration of tuber bulking). Note that variable on Y-axis (i.e. $A_{sum}$: area under whole green canopy cover curve) is considered equivalent to maturity, see text.

by criterion based on trait $D_{P2}$ (i.e. $R^2 = 0.77$). These results were in line with our path coefficient analysis conclusions (Fig. 4.2). These results concluded that overall, most of the physiological maturity type criteria were fully capable of reproducing the maturity type of genotypes across diverse environments.

### 3.6. Direct/indirect selection possibilities for maturity type

Figure 4.7 illustrates the relationships between maturity scores (Table 4.1) from different maturity type criteria within the F1 population across all six experiments. All correlations were highly significant ($P<0.01$) and positive.

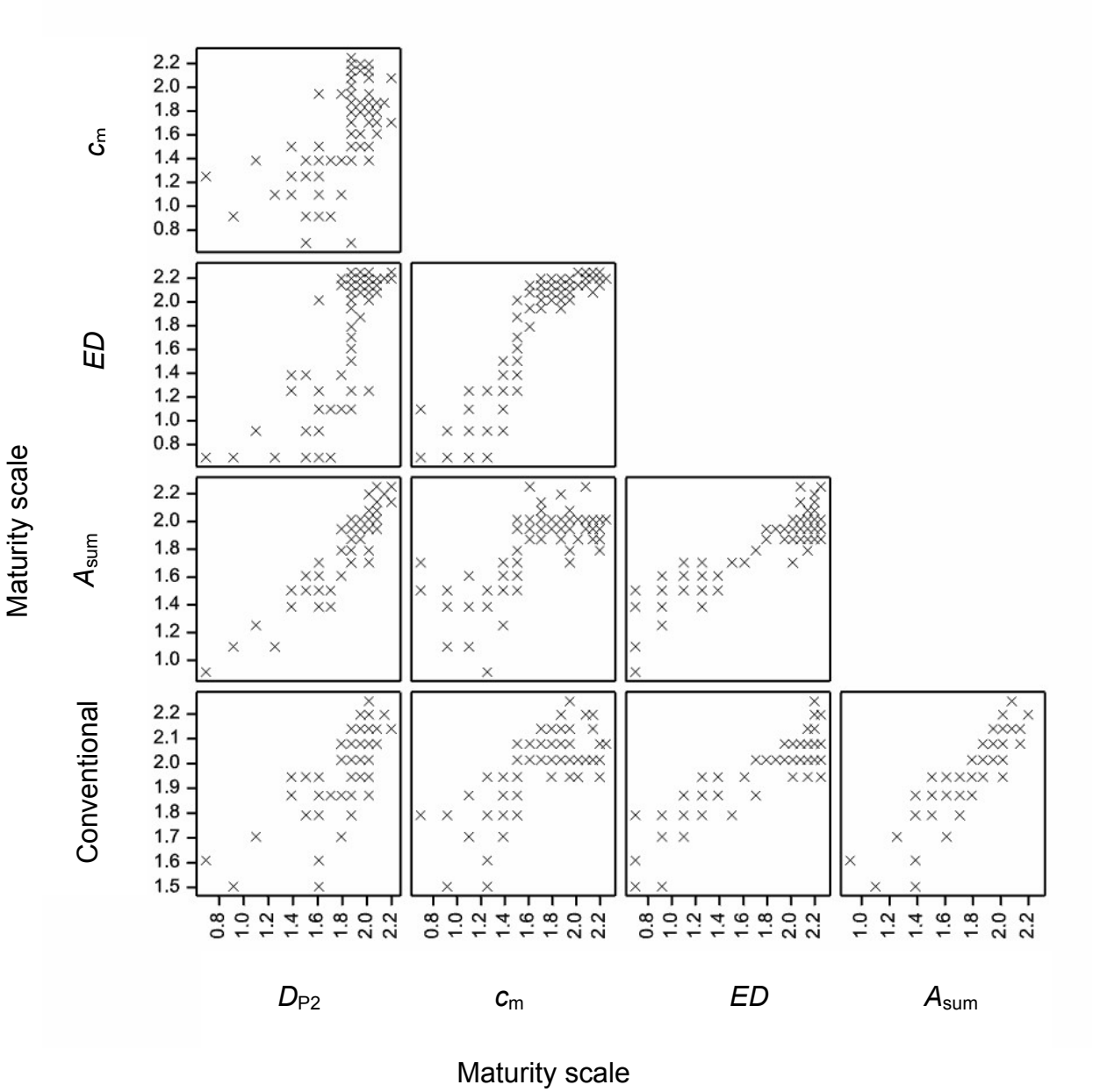


**Figure 4.7.** Relationships between maturity scale values from different maturity type criteria within F1 population across six environments. Values on the X-axis and Y-axis represent log-transformed maturity scales (cf. Materials and Methods).

The results indicated very strong phenotypic correlations between the $A_{sum}$ criterion and $D_{P2}$ and *ED*, and between $c_m$ and *ED* criteria ($r$= 0.89). This shows that both rate and duration of tuber bulking are important in controlling the total duration of crop growth and the capacity of the crop to intercept radiation, crucial in determining final yield (Kooman and Rabbinge, 1996). These results indicated that maturity type of the genotypes based on $A_{sum}$ could be indirectly obtained by selecting genotypes with the proper $D_{P2}$ criterion. Our results in previous chapters (2 and 3) showed that quantitative trait loci (QTL) for these physiological traits are

mostly co-localised on chromosome V of the paternal (i.e. RH) genome in the F1 segregating population of potato and explain more than 50% of the total phenotypic variance. Moreover, our results in Chapter 2 indicated that maximum QTL additive effects were associated with $A_{sum}$ throughout different environments (see Fig. 2.12), illustrating the close association of maturity with this physiological trait. Therefore, this locus could be used as an explanatory variable for further elucidating the physiological as well as genetic aspects of maturity in potato. The conventional criterion on account of its subjective nature does not explain maturity type any further, in spite of its high correlation with some of the physiological maturity type criteria.

### 3.7. Applications of re-defining maturity type based on physiological traits

Our study showed that re-defining the maturity type on the basis of physiological traits is useful. The new physiology-based maturity definition could be applied in plant breeding and in crop management (Struik, 2010).

The physiological maturity criteria can play a significant role in devising crop escape strategies to cope with biotic stresses, such as late blight (Struik, 2010). Strategies like advancing the crop growth before the stress becomes too harmful may prove very useful. For instance, genotypes with early tuber set and faster tuber bulking can better escape the disease severity. The physiological based maturity criteria may also allow the selection of the genotypes for maturity type in order to break the correlation between resistance and late maturity. Characteristics that could be useful indicators of competitive ability against weeds may include a growth habit that allows early attainment of full canopy cover and its presence for longer periods (i.e. genotypes with high $D_{P2}$ and late maturity (e.g. high $A_{sum}$) (Joenje and Kropff,1987; Lotz et al.,1991; Grevsen, 2003; Williams et al., 2008). This can help potato growers to choose those genotypes with a high tolerance to weed pressure and able to maintain high yields in the presence of weeds, especially in organic agriculture. In this context, inclusion of maturity type based on physiological characters in breeding programmes could allow the selection of competitive genotypes in field conditions where weeds are always present as well as enhance the efficacy of overall weed control.

The physiological maturity type criteria would also give more insight into the physiological nature of genotype's maturity type and therefore would help in proper planning of haulm killing. This would give the benefits of increased tuber quality (Halderson et al., 1985) and economical savings (cost of desiccant).

The physiological maturity type criteria take into account the quantitative knowledge of the influence of environmental factors on the length of the growing

season and on dry matter partitioning, necessary for designing genotypes for such environments (Haverkort and Kooman, 1997). Our approach therefore would help in designing strategies for breeding for genotypes with specific maturity type.

## 4. Conclusions

In this chapter we tried to create a clear definition of maturity type and to develop a quantitative, reproducible method to assess the maturity type in a large set of potato genotypes. We presented an approach whereby potato physiological traits were used to explain the maturity type in a set of varieties covering a wide range of maturity types and a well-adapted diploid F1 segregating population. This procedure resulted in four re-defined criteria of defining maturity type which we call "physiological maturity type criteria" as opposed to the conventionally used criterion.

The physiological maturity type criteria were based on physiological and quantitative knowledge and were easily interpretable in terms of physiological trade-offs that existed between the selected traits. The conventional maturity type criterion could not offer this advantage on account of its subjective and ordinal nature. Our results showed that the conventional maturity criterion showed considerable overlapping among the maturity classes with maximum variability. Besides, it could not offer a clear definition of maturity on account of its subjective nature. In contrast, physiological maturity type criteria tended to explain maturity type in potato more clearly and were better capable of predicting the maturity type of genotypes across diverse environments than the conventional criterion.

This study gave more understanding about the nature of genotype's maturity type, besides, it also highlighted the complexity of defining maturity type in a potato. Our results however, showed that re-defining the maturity type of a large set of genotypes on the basis of physiological traits is possible and may prove useful. A new physiology-based maturity definition could offer wider applications in potato breeding and crop management studies. This new criterion may be amenable to further genetic analysis and could also help in designing strategies for potato ideotype breeding for genotypes with specific maturity type for specific growing conditions and/or environments.

# CHAPTER 5

## An ecophysiological model analysis of yield differences within a set of contrasting cultivars and an F1 segregating population of potato (*Solanum tuberosum* L.) grown under diverse environments*

M.S. Khan, X. Yin, P.E.L. van der Putten, P.C. Struik

**Abstract**

We tested the capability of the generic ecophysiological model 'GECROS' to analyse differences in tuber yield of potato in a set of cultivars covering a wide range of maturity types and a diploid F1 population segregating for maturity type. The model predicts crop growth and development as affected by genetic characteristics and climatic and edaphic environmental variables. The genotype-specific model-input parameter values were estimated and the model was used for predicting the tuber yield of an F1 population, their parents and a set of cultivars in multiple field experiments. The model yielded a reasonably good prediction of differences in tuber yield across environments and across genotypes. Trends of growth and nitrogen uptake were adequately reproduced by the model. Model analysis identified the genotypic key-parameters affecting tuber yield production and $N_{max}$ (i.e. total crop N uptake) contributed most to the determination of tuber yield. Genotypes with higher $N_{max}$ and lower tuber N concentration exhibited higher tuber dry matter yield. These results were largely confirmed by statistical path coefficient analysis. GECROS model is a useful tool in analysing the contribution of individual physiological traits to yield across different environments. Such information can greatly facilitate the development of potato ideotypes for specific environments.

**Key words:** Potato (*Solanum tuberosum* L.); ecophysiological crop model; GECROS; genotype-by-environment (G×E) interaction; complex traits; yield; sensitivity analysis; path coefficient analysis; ideotype; plant breeding.

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* *To be submitted.*

## 1. Introduction

Potato (*Solanum tuberosum* L.) is one of the most important and widely cultivated non-cereal crops, in many parts of the world (Walker et al., 1999; Hijmans, 2001). Due to increasing food demand and changing diets potato is becoming a subsistence crop in many growing areas. There is a need to increase potato yield via genetic improvement and/or altered crop management. In order to efficiently improve the target traits, prediction of the phenotypic characteristics of genotypes under various environmental conditions is crucial (Asseng and Turner, 2007).

Most agronomic traits are genetically complex (Daniell and Dhingra, 2002; Lark et al., 1995; Orf et al., 1999; Stuber et al., 2003); they have low heritability, are strongly dependent on environmental changes and often show high genotype-by-environment (G×E) interactions (Allard and Bradshaw, 1964; Tardieu, 2003; Cooper et al., 2002, 2005). There is a need to dissect complex traits like yield into simpler characters and to separate factors influencing a given phenotypic trait and shifting from highly integrated traits to genotype-specific traits (Yin et al., 2002). Ecophysiological crop growth models have the potential to assess a complex trait at a higher organizational level, via integrating the information about processes at the lower level. Their ability to incorporate knowledge of physiological traits to simulate crop growth and yield as influenced by growing environment, and agronomic practices suggests the possibility of using models as a crop breeding tool (Boote and Tollenaar, 1994; Aggarwal et al., 1997; Bastiaans et al., 1997; Boote et al., 1998; Uehara, 1998; White, 1998; Boote et al., 2001; Mavromatis et al., 2001, 2002; Hammer et al., 2002, 2006; Tardieu, 2003; Banterng et al., 2004; Hoogenboom et al., 2004; Yin et al., 2004; Asseng and Turner, 2007; Herndl et al., 2007; Letort et al., 2007).

One of the main applications of these models is to describe the differences in yield potential of genotypes between or within a breeding population on the basis of individual physiological parameters. These parameters could be considered as quantitative traits and are amenable to further analysis (Yin et al., 2004; Quilot et al., 2005), e.g. for evaluating and designing ideotypes (Loomis et al., 1979; Kropff et al., 1995; Boote et al., 1996; Cilas et al., 2006; Yin et al., 2003c, 2004; Yin and Struik, 2008). This is possible because these parameters, often regarded as 'genetic coefficients', are specific to each genotype and supposed to be constant under a wide range of environmental conditions (Boote et al., 2001; Tardieu, 2003; Bannayan, 2007). This model feature makes it possible to make predictions about the plant developmental processes of genotype in a wide range of environments (Stam, 1996; Bindraban, 1997; Hoogenboom et al., 1997). Such models can quantify crop genotype-phenotype relationships (Yin et al., 2000b, 2004; Reymond et al., 2003; Hammer et al., 2006) and therefore are highly suitable for studying the G×E (Shorter et al., 1991;

Hunt, 1993; Kropff and Goudriaan, 1994; Hammer et al., 1996; Chapman et al., 2002; Yin et al., 2003c; Banterng et al., 2004, 2006; Yin et al., 2004; Suriharn et al., 2007) and could assist with multi-location evaluation of crop breeding lines (Liu et al., 1989; Aggarwal et al., 1995; Palanisamy et al., 1995; Piper et al., 1998; Boote et al., 2001; Slafer, 2003; Banterng et al., 2004; Mayes et al., 2005). For potato, Kooman and Spitters (1995) showed that simulation models can be useful for predicting tuber yield and gaining insight into crop growth processes and can help to explore options for crop improvement.

However, traditionally, crop models have principally been used to study and predict crop performance in response to environmental conditions and management practices, whereas genotypic impacts on crop performance (especially in the context of plant breeding where large numbers of genotypes are involved) have received less attention. This is partly due to the constraints imposed by time, resources, and large number of genotypes that makes it difficult to measure detailed growth dynamics to fully derive the genotype-specific model coefficients (Anothai et al., 2008), and partly due to the restricted capabilities of models to represent genetic differences (White and Hoogenboom, 1996; Hoogenboom et al., 1997).

To be useful, the physiological frameworks used for trait dissection and modelling at whole-crop level must realistically capture the functional basis of the genetic variation for complex traits of interest (Yin et al., 2000b). Most existing crop models, which were constructed to deal mostly with agronomic issues, are not well structured in this regard for instance for capture and use of nitrogen (N) (Jeuffroy et al., 2002) and for carbon (C) and N partitioning (Dingkuhn, 1996). They also lack the ability to describe subtle complexities associated with the differences between genotypes (White and Hoogenboom, 1996; Yin et al., 2004).

In this respect, crop physiological modes of action of the complex trait must be understood and quantified and the crop model must be sufficiently detailed to simulate the consequences on growth and development generated by the genotype (G), environment (E) and ultimately G×E (Hammer et al., 1996). To become effective tools for addressing G×E, existing models have to be improved, both in terms of model structure and input parameters (Yin et al., 2004; Yin and Struik, 2008). Studies are thus needed to develop and/or test the potential capabilities of current crop models for plant breeding and to specify the necessary modifications for such applications.

The objectives of this study are (i) to examine the ability of a recent ecophysiological crop growth model 'GECROS' to explain yield differences among 100 genotypes from an F1 segregating population, their parents and a set of standard cultivars of potato, and (ii) to analyse the relative importance of individual

physiological traits in determining yield differences. These analyses could have a strong implication in exploring the extent to which our model dissects the role of G, E, and G×E on tuber yield production, and in designing strategies for potato ideotype breeding for specific environments.

## 2. Materials and methods

### 2.1. *The GECROS model*

The model GECROS (Genotype-by-Environment interaction on CROp growth Simulator) is a generic ecophysiological model that predicts crop growth and development as affected by genetic characteristics and climatic and edaphic environmental variables. For a detailed description of the model, see Yin and Van Laar (2005). Here, only the key processes modelled in GECROS (version 2.0 as used by Yin and Struik, 2010) are summarised.

Coupled modelling of $CO_2$ diffusional (stomatal and mesophyll) conductance, leaf photosynthesis and transpiration in dependence of leaf nitrogen content is implemented according to Yin and Struik (2009). Subsequently, the results are integrated for the whole canopy, based on the sun/shade approach of De Pury and Farquhar (1997). The Gaussian integration is used to extend the instantaneous rates into the daily total photosynthesis and transpiration.

Daily crop respiration is simulated based on the theoretical framework of respiration components: (i) growth respiration, (ii) respiration for ammonium and nitrate uptake and nitrate reduction; uptake of other ions, phloem loading, and (iii) residual maintenance respiration (Cannell and Thornley, 2000).

Nitrogen demand is modelled as the maximum value of the deficiency-driven and the growth activity-driven demand. The first guarantees the actual plant N concentration being above a critical value; the second is modelled based on the optimum N-C ratio for maximising the relative carbon gain, using the equation of Hilbert (1990). The actual N uptake is limited by the maximum daily N supply rate from the soil.

Partitioning of the newly produced C and absorbed N is modelled in two steps: first, between the root and the shoot, and then among organs within the shoot. Root-shoot partitioning for C and N responds to environmental conditions, based on the root-shoot functional balance theory (e.g. Charles-Edwards, 1976) adjusted in order to maximize relative growth rate.

Intra-shoot carbon partitioning to the structural stems and to the tubers are

determined according to their expected daily carbon demands, which are described by the differential form of a sigmoid function for asymmetric determinate growth (Yin et al., 2003a). In the model, the potential tuber sink size is calculated from the estimated amount of N available for tuber growth. The remaining shoot-carbon goes either to the leaves or to the C reserve pool, depending on whether the green-surface area index becomes C- or N-limited.

The intra-shoot N partitioning is based on pre-defined maximum tuber N concentration ($n_{SO}$, which is a genotype-specific parameter, Table 5.1) and minimum N concentration in the stems. If the N requirements for the tubers and structural stems are met from the current N uptake, the remaining shoot N goes to the leaves, which include the photosynthetically active green surfaces of other organs. If the requirements for the tubers are not met, remobilisation of N first from the reserves and then from the leaves and the roots takes place, until the reserves are depleted and the N concentrations in the leaves and roots reach their minimum values. This remobilisation results in leaf and root senescence, reflecting the phenomenon of so-called '*self-destruction*' (Sinclair and De Wit, 1975). If the tuber N requirements are not met by shoot N and remobilization, the tuber N concentration declines.

Green-surface area index is modelled as the minimum value of C-limited and N-limited areas. The underlying principle is described in detail by Yin et al. (2000c, 2003b). As such, senescence of leaves is computed as a function of N reduction in the canopy. Similarly, senescence of roots depends on N reduction in the roots.

Daily phenological development rate ($\omega_i$), which has a unit of $d^{-1}$, is calculated both for the pre-tuberisation period and for the tuber bulking period, respectively, using genotype-specific parameters $m_V$ and $m_R$, representing the pre-tuberisation phase and the duration between onset of tuber bulking and crop maturity, respectively (Table 5.1). Phenological response to temperature is based on a flexible bell-shaped non-linear beta function (Yin et al., 1995). This function is implemented on an hourly basis to account for the diurnal temperature fluctuation. Values of the cardinal temperatures in this function were taken from Chapter 2 for potato.

In the model, plant height is required mainly for calculating the carbon demand for structural stems. Plant height is modelled to follow a sigmoid pattern, assuming that maximum plant height ($H_{max}$, Table 5.1) is reached at a midway between tuber bulking and crop maturity. The increment of plant height is decreased if available carbon assimilates do not meet the potential carbon demand for stem growth.

GECROS runs with a time step of one day. Required daily weather data include minimum and maximum temperature, global solar radiation, vapour pressure, wind speed, and rainfall. Air $CO_2$ concentration should be provided. Other required inputs are daily supply of water and N available for crop uptake.

### 2.2. *Experimental data*

Datasets for our model analysis came from six field experiments, performed in Wageningen (52˚ N latitude), the Netherlands, with two experiments in each year, i.e. 2002 (Exps 1 and 2), 2004 (Exps 3 and 4), and 2005 (Exps 5 and 6) (For details see Chapters 2 and 3). These experiments differed in environmental conditions because they were carried out in different years, on different soils and under different nitrogen (N) fertiliser regimes, thereby creating six contrasting environments. The plant material for these experiments consisted of 100 F1 diploid (2n = 2x = 24) potato genotypes derived from a cross between two diploid heterozygous potato clones, SH83-92-488 × RH89-039-16, hereafter referred to as the 'SH × RH population' (Rouppe van der Voort et al., 1997; Van Os et al., 2006). This population segregates for maturity type (Van der Wal et al., 1978; Van Oijen, 1991). Besides, five standard cultivars (viz. Première, Bintje, Seresta, Astarte and Karnico) were also included on the basis of their maturity type under Dutch conditions.

To evaluate model performance in representing growth dynamics, field measurements were performed on few genotypes during year 2004 (Exps 3 and 4), and 2005 (Exps 5 and 6). A total of five harvests were carried out at intervals of 1-2 weeks during the crop period. At least four representative plants per sampling point were taken and measurements were made on both above- and below-ground plant parts for dry matter and N content in different plant parts. To determine the dry weight, the plants were divided into their constituents of living and dead leaves, stems, stolon, and tubers, and sub-samples of each portion were dried at 70 ˚C to a constant weight. Roots were not measured since they are difficult to harvest (Kooman, 1995). Further sub-samples were used to determine nitrogen content by means of micro-Kjeldahl digestion and distillation.

To measure the model predictability for the full set of 100 genotypes, tuber dry matter was measured at only three harvests during the growing period and tuber N content was measured at maturity (see Materials and Methods, Chapter 3). These data sets created the basis for the estimation of genotype-specific parameters and for model testing as described later. In addition, green canopy cover (%) was visually assessed on weekly basis during the whole crop cycle for all genotypes (Chapter 2).

### 2.3. *Estimation of model parameters*

Table 5.1 gives the description of genotype-specific parameters of GECROS, which include total crop N uptake at maturity ($N_{max}$). $N_{max}$ *per se*, as an accumulative quantity in the crop life cycle, should not have been considered as an input parameter. However, there was not sufficient information about the soil and modelling of soil

**Table 5.1.** List of genotype-specific parameters of GECROS model (See Materials and Methods, section 2.3). *td* stands for thermal day.

| Trait | Description | Unit |
|---|---|---|
| $m_V$ | Period from plant emergence to onset of tuber bulking | *td* |
| $m_R$ | Duration between onset of tuber bulking and crop | *td* |
| $H_{max}$ | Maximum plant height | m |
| $n_{SO}$ | Maximum tuber N concentration | g N $g^{-1}$ DM |
| $N_{max}$ | Total crop N uptake at crop maturity | g N $m^{-2}$ |

processes is usually full of uncertainties. To reduce an influence of large uncertainties in predicting edaphic variables for N supply, we took a simple approach, using $N_{max}$ as a model-input parameter. The value of $N_{max}$ was estimated on the basis of the assertion that the distribution of N over tubers and other components is probably fairly conservative (Biemond and Vos, 1992), assuming that N accumulation in tubers and haulm accounts for 77.5% and 15% (own measured data on few genotypes), and N accumulation in the roots for 7.5% (see data of Sharifi et al., 2005), of $N_{max}$. Procedures for estimation and correction for experiment-specific parameter values are described below.

Of the five parameters, values of phenological parameters $m_V$ and $m_R$ were derived from Chapters 2 and 3, where using the afore-mentioned data sets, we analysed the dynamics of potato canopy cover development and tuber bulking, respectively as a function of thermal time. Chapter 2 describes the three phases of canopy cover development (i.e. build-up phase, maximum cover phase, decline phase), using biologically meaningful component traits. The end of the canopy build-up phase is marked by $t_1$ at which the canopy cover attains its maximum level (see Fig. 2.1 in Chapter 2). The end of canopy senescence (or crop maturity) is marked by $t_e$. In Chapter 3, we quantified the tuber growth during exponential and linear phases, in which $t_B$ characterises the onset of linear phase of tuber bulking (see Fig. 3.1 in Chapter 3).

For few genotypes with more data for growth dynamics, availability of sufficient data points allowed the estimation of $m_V$ as $t_B$. However, for other genotypes, the pre-tuberisation phase $m_V$ is hard to estimate accurately. A sensitivity analysis showed that this trait mattered little for model prediction of tuber yield (see Results), we assumed that $m_V = t_1$. Because $t_1$ is sensitive to the environmental variation (see Fig. 2.7), and Exp 6 showed comparatively lower variation for $t_1$ (Chapter 2), values of $t_1$

based on Exp 6 were used for genotype-specific $m_V$. Parameter $m_R$ was calculated as ($t_e$-$m_v$). Here again, in order to reduce the random noise, mean $t_e$ per F1 genotypes across six experiments was used for estimating $m_R$.

Not surprisingly, values of plant height, tuber N concentration, and total crop N uptake differed among the experiments (Fig. 5.1). To reduce the influence of environmental noise yet reflect the differences among the experiments, $H_{max}$, $n_{SO}$, and $N_{max}$ were estimated as across-experiment mean times a correction factor per individual experiment. The correction factor was calculated as a slope of the regression line between experiment-specific parameter values versus its across-experiment mean. In the case of Exps 1 and 2, for which we lacked the data for parameters $n_{SO}$, $H_{max}$ and $N_{max}$ (Fig. 5.1), combined information from other experiments for these parameters was used, with the correction factor obtained from the slope of the regression between observed tuber yield per Exps 1 or 2 versus mean observed tuber yield across the other four experiments.

Crops were not subject to any water stress during the growth; so, a high value of daily water supply from soil was given for simulation to mimic no drought stress. Daily N supply from soil was derived from $N_{max}$, based on the fitted pattern of the dynamics of the accumulative crop N uptake as observed for the few genotypes with the detailed measurements.

### 2.4. *Model analysis to identify major yield-determining traits*

Sensitivity analysis was performed to determine the importance of individual genotype-specific parameters in determining tuber yield potential. Data sets from Exps 3-6 were used for this purpose. We followed the approach of Yin et al. (2000b, 2005). First, the baseline simulation was conducted, where all genotype-specific parameter values were used as input for simulation. Then, parameters were fixed, one at a time, at their across-genotype mean. The extent, to which the percentage of variance explained by the model was decreased relative to the percentage explained by the baseline simulation, was used to rank the relative importance of the parameters in determining tuber yields.

### 2.5. *Statistical path coefficient analysis*

To confirm the result of ecophysiological modeling analysis, path coefficient analysis was performed, also to check out the important direct and indirect inter-associations between the genotypic-specific parameters and final tuber yield. This analysis was

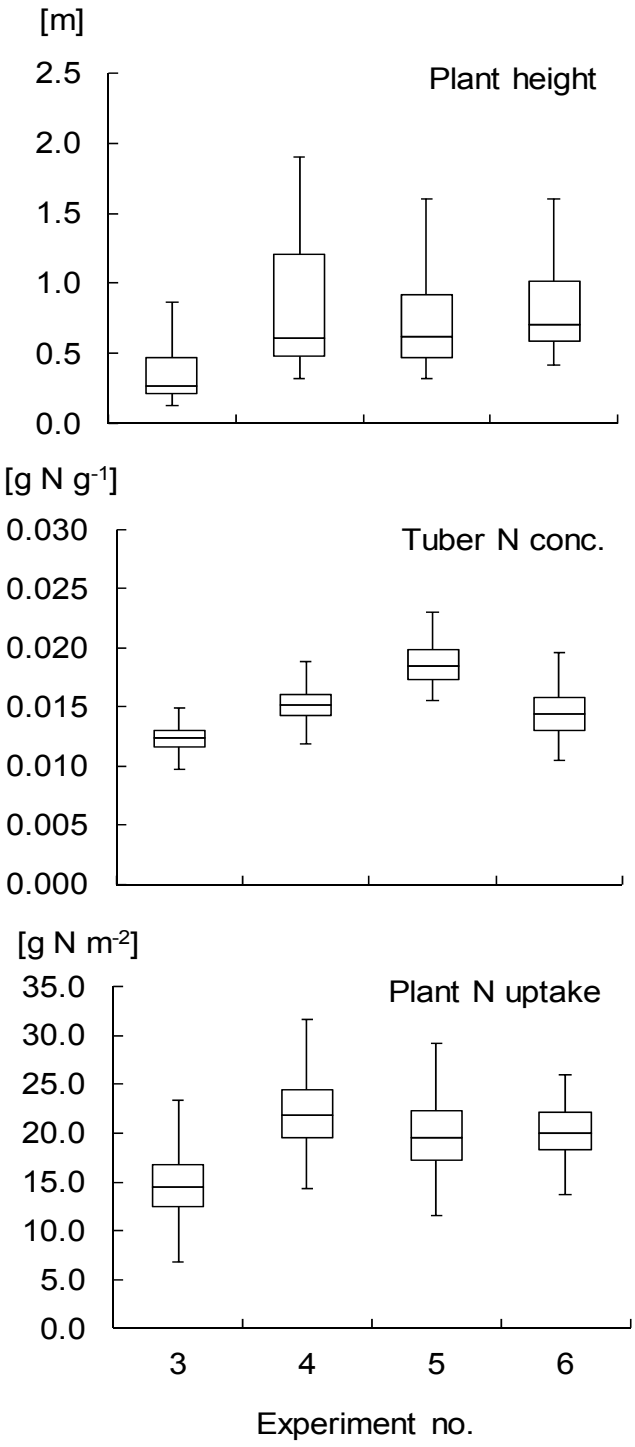


**Figure 5.1.** Box plots of means of an F1 population for three measured parameters in four experiments. The boxes span the interquartile range of the trait values, so that the middle 50% of the data lay within the box, with a horizontal line indicating the median. Whiskers extend beyond the ends of the box as far as the minimum and maximum values. Points were missing for Exps 1 and 2 because these traits were not measured therein (see the text).

performed on the mean of F1 genotypes across environments following the procedure of Chapter 3.

## 3. Results and discussion

### 3.1. *Model parameters*

The evaluation of genotype-specific model parameters indicated that there were strong genetic differences among the standard cultivars (Table 5.2). As expected, values of most of these parameters except $n_{SO}$ were higher for late maturing cultivars (Astarte and Karnico) than for mid-late (Seresta), mid-early (Bintje), and early cultivars (Première). In contrast, values of $n_{SO}$ were higher for early maturing cultivars like Première followed by mid-late and late cultivars (Table 5.2). It has been found in previous research that N uptake and use efficiency differ by cultivar (Johnson et al., 1995; Kleinkopf et al., 1981; Lauer, 1986; Porter and Sisson, 1991a,b). Early-maturing cultivars stop leaf growth earlier than late-maturing cultivars and therefore exhibit less vegetative growth and a shorter tuber bulking period. This pattern results in lower N use efficiencies and higher tuber N concentrations in earlier genotypes (Vos, 1997; Chapter 3).

The results for the F1 population indicated that most of the parameters were nearly normally distributed, apart from $m_R$ and $H_{max}$ for which the distribution was bimodal (Fig. 5.2). The F1 population displayed transgressive segregation, with more extreme values in the population than their parents (SH and RH).

**Table 5.2.** Estimated mean values of genotype-specific parameters for five standard cultivars (listed in order of increasingly longer crop cycle). *td* stands for thermal day. (–) represents lack of data. See Table 5.1 for parameter descriptions.

| Cultivar | $m_V$ (*td*) | $m_R$ (*td*) | $H_{max}$ (m) | $n_{SO}$ (g N g$^{-1}$ DM) | $N_{max}$ (g N m$^{-2}$) |
|---|---|---|---|---|---|
| Première | 13.3 | 36.7 | 0.53 | 0.018 | 21.9 |
| Bintje | 14.4 | 51.1 | 0.82 | 0.017 | 25.8 |
| Seresta | 17.7 | 57.4 | 1.05 | 0.014 | 25.4 |
| Astarte | 15.1 | 65.1 | 1.14 | 0.013 | 24.6 |
| Karnico | – | – | 1.39 | 0.012 | 25.8 |

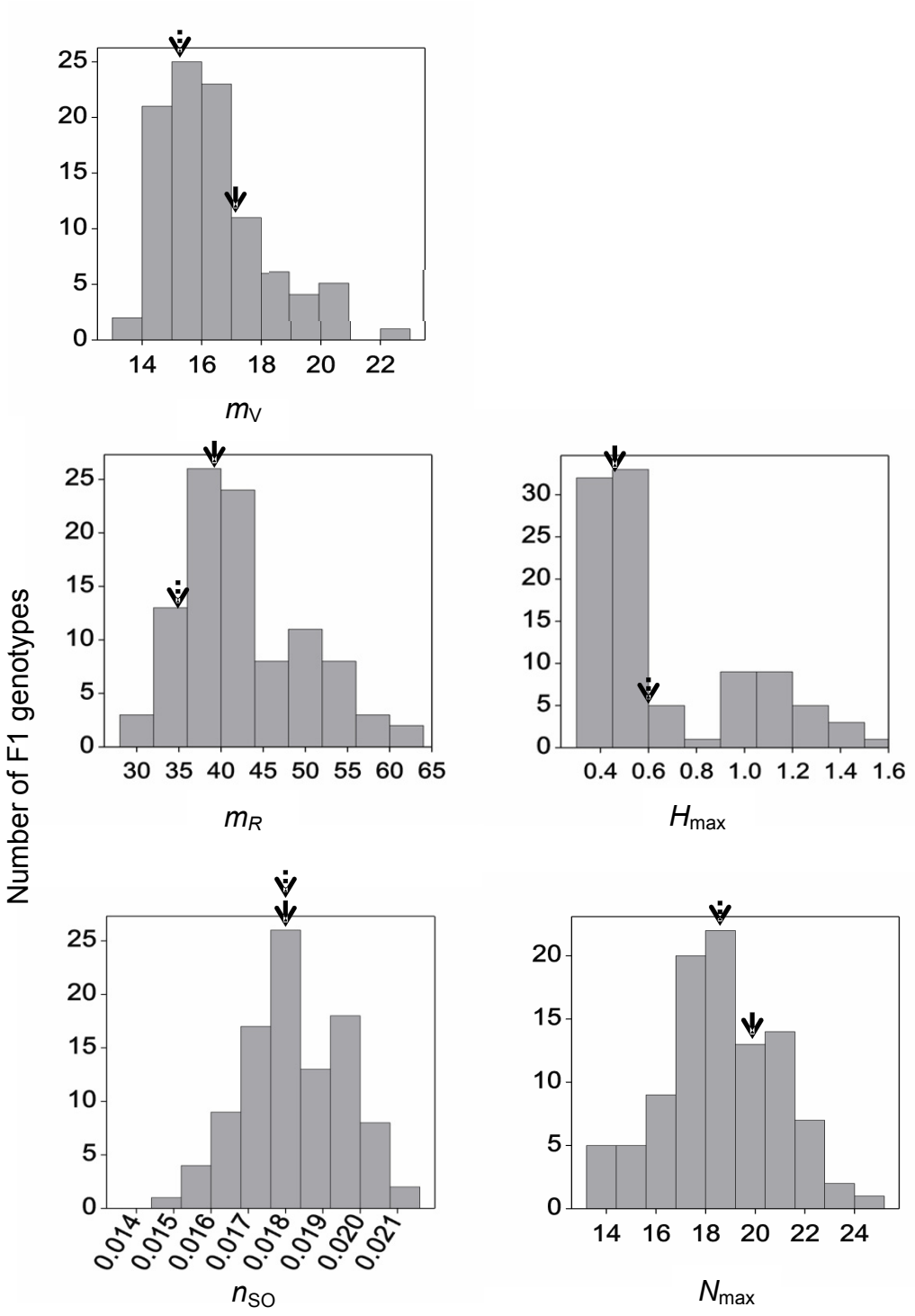


**Figure 5.2.** Distribution of genotype-specific parameters of GECROS model for 100 F1 genotypes. The values of two parents 'SH' and 'RH' are indicated by full arrow and dashed arrow, respectively. See Table 5.1 for parameter descriptions.

### 3.2. *Model performance in representing growth dynamics*

The GECROS model efficiently simulated the dynamics of important potato physiological growth processes under a range of environmental conditions. Here we present the results of two experiments of 2004 (i.e. Exps 3 and 4). These experiments were low and high in N availability, respectively (Fig. 5.1; Chapter 2). Figure 5.3 presents modelled and observed data of plant and tuber N uptake and dry matter for the two parental genotypes. Model evaluation showed good agreements between observed and simulated growth pattern of these processes.

The N accumulation in tubers showed an S-shaped growth pattern, in contrast to the pattern of plant N uptake (Fig. 5.3). The results further showed that at the beginning of the season the tuber dry matter was underestimated while plant dry matter was estimated rather well, whereas at the end of the season the simulated tuber dry matter yields compared well with the measured data. The current data (Fig. 5.3) also indicated that the tuber as well as plant dry matter is reduced when N is limiting (i.e. Exp 3), most likely via limited leaf expansion and interception of radiation (Vos and Biemond, 1992).

### 3.3. *Model performance in explaining yield differences among genotypes*

To evaluate the model's ability to reproduce the observed yield-based variation, differences in the actual and modelled yield were compared across different environments for the F1 population, their parents and a set of standard cultivars. Overall, the model adequately simulated differences in tuber yields among these genotypes in all experiments (Fig. 5.4). However, there were discrepancies between simulated and measured tuber yields, especially in Exp 3, where the predicted tuber yield was under-estimated in high-yielding, and over-predicted in low-yielding genotypes. With the concept used in GECROS for tuber N accumulation, the fraction of tuber N is a very sensitive input parameter, not only affecting the final N concentration, but also the harvest index and the potential tuber yield (Yin and Van Laar, 2005).

The model explained variations in the tuber yield, with $R^2$ ranging from 35% to 65% for the F1 population, and 80% to 96% for the parents and five standard cultivars, among the Exps 3-6 (Fig. 5.4). However, in case of Exps 1 and 2, the model could not satisfactorily explain the variation in the tuber yield (Fig. 5.4). This is because there was a lack of information about N availability and therefore assumptions had to be made for defining the related input parameters for those experiments (see Materials and Methods).

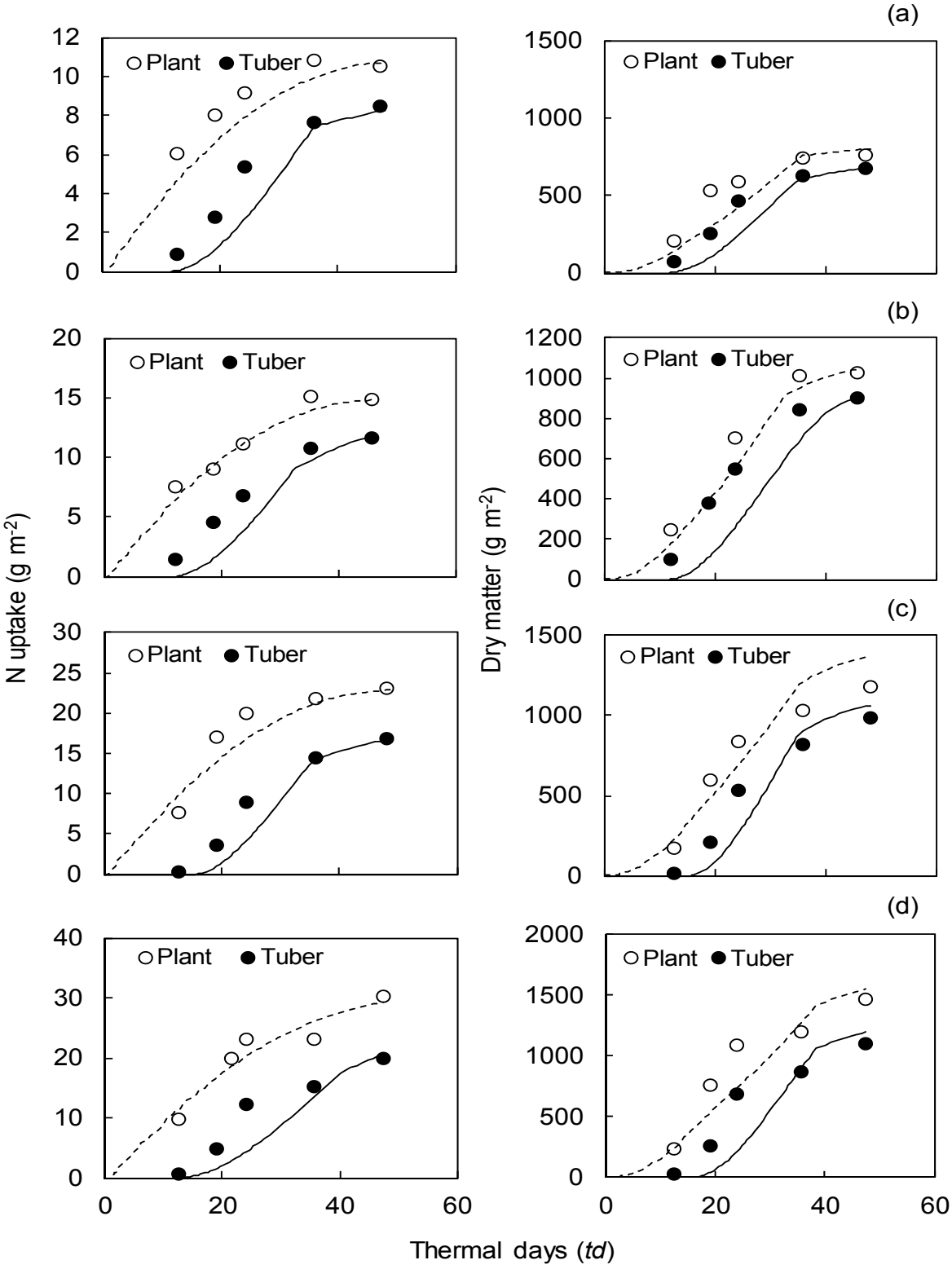


**Figure 5.3.** Modelled (lines) and observed (symbols) for genotypes (a) SHRH-469 and (b) RH89-039-16, in Experiment 3, and (c) SHRH-469 and (d) RH89-039-16, in Experiment 4, performed during 2004.

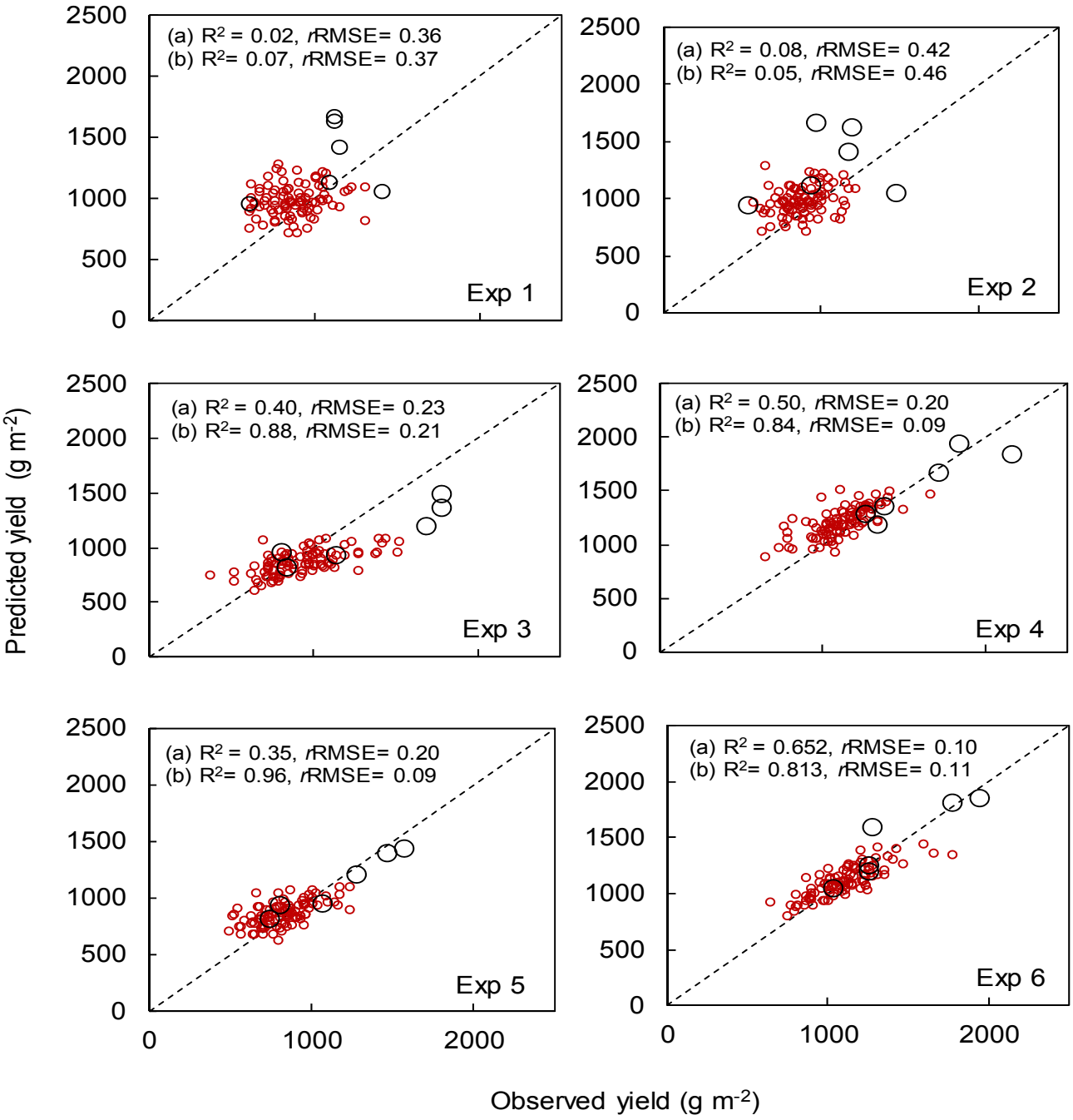


**Figure 5.4.** Comparison between predicted and observed tuber yield for (a) 100 F1 genotypes (small circles), (b) 5 standard cultivars and 2 parental genotypes (SH and RH), tested per each individual experiment (large circles). $R^2$ values were obtained from a linear regression; *r*RMSE is the relative RMSE, calculated as the root-mean-square error divided by the mean observed tuber yield.

The model also predicted well (i.e. $R^2$ = 86%) the mean tuber yield across four environments (i.e. Exps 3-6) (Fig. 5.5a). Furthermore, the model satisfactorily predicted variation in the mean tuber yield across the F1 genotypes among the environments (Fig. 5.5b). The model predicted 57% of the total observed variation, when all observations for the F1 genotypes in the four environments were pooled (Fig. 5.5c).

The model performance was also evaluated by calculating the relative root mean square error (*r*RMSE; Figs 5.4-5.5). The *r*RMSE values ranged from 0.10 to 0.42 in F1 population and 0.09 to 0.46 for the two parents and five standard cultivars, among the Exps 3-6 (Fig. 5.4). As expected, the *r*RMSE values were higher for the first two experiments (Exps 1 and 2) mainly due to lack of good fit as described earlier. In other experiments, *r*RMSE values were reasonably good. The results further indicated low *r*RMSE values for the mean tuber yield across-environments (i.e. 0.09), across the F1 genotypes among the environments (i.e. 0.06), and when all observations for the F1 genotypes in the four environments were pooled (i.e. 0.17) (Fig. 5.5).

Overall, our results indicated that using as few as five measured genotype-specific parameters (Table 5.1), the GECROS model showed a good potential in explaining the observed yield differences among genotypes.

### 3.4. *Model-based sensitivity analysis to identify important yield-defining traits*

Ecophysiological models can serve as an important tool to determine model input parameters critical for yield potential (Yin et al., 2000b). Sensitivity analysis was performed to evaluate the importance of individual genotype-specific parameters in determining tuber yield potential. The results of the baseline simulation, in which genotype-specific values were applied for all model-input parameters, were already presented in the previous section for individual experiments (Fig. 5.4). When the parameters were fixed, one at a time at their across-genotype mean, the model explained percentage variance dropped from the baseline simulation for most of the parameters throughout the environments (Table 5.3). This reduction in variance explained was more evident for $N_{max}$ followed by $n_{SO}$ throughout the experiments. For other parameters, in some cases, the percentage variance accounted for was even higher than that obtained from the baseline simulation. This was evident for $m_V$ in Exps 3, 4, and 5 and $H_{max}$ in Exps 3 and 6. Almost similar trends were recorded for observations in across-environment means as well as when data were pooled. These results conclude that the relative importance of parameters for tuber yield determination can be ranked as: $N_{max} > n_{SO} > m_R > m_V$ and $H_{max}$. Obviously, $N_{max}$ and $n_{SO}$ were the most important parameters as they contributed most to the

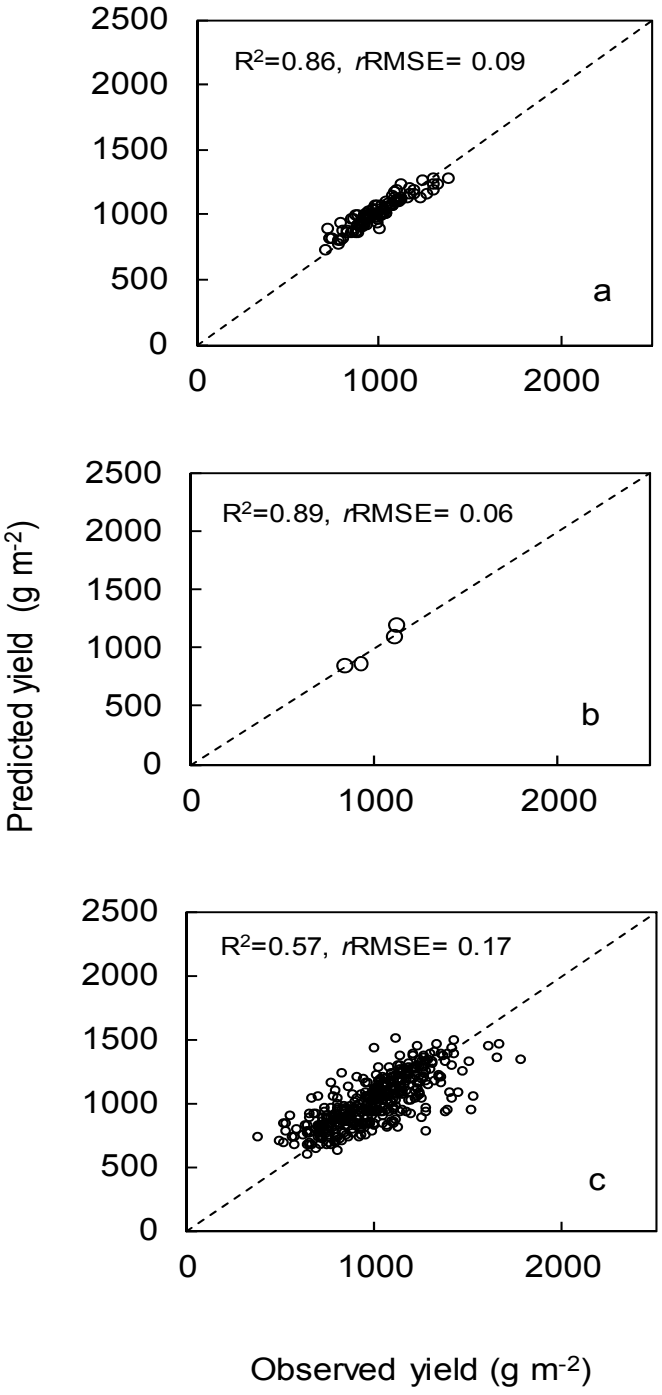


**Figure 5.5.** Comparison between predicted and observed tuber yield (g $m^{-2}$) tested in across-environment mean of 100 F1 genotypes (*n* = 100 points) (a), in across-genotype mean of four environments (i.e. Exps 3-6) (b), and when data from 100 genotypes tested in the four experiments are pooled (*n* = 400) (c). $R^2$ values were obtained from a linear regression; *r*RMSE is the relative RMSE, calculated as the root-mean-square error divided by the mean observed tuber yield.

**Table 5.3.** Percentage of the observed tuber yield variation in four experiments (Exps 3-6) of F1 population of potato accounted for by the GECROS model when different sets of values for five genotype-specific parameters were used. See Table 5.1 for parameter descriptions.

| Set of parameters [a] | | | | | $R^{2b}$ | | | | $R^{2c}$ | $R^{2d}$ |
|---|---|---|---|---|---|---|---|---|---|---|
| $m_V$ | $m_R$ | $H_{max}$ | $n_{SO}$ | $N_{max}$ | Exp. 3 | Exp. 4 | Exp. 5 | Exp. 6 | | |
| + | + | + | + | + | **0.40** | **0.50** | **0.35** | **0.65** | **0.86** | **0.57** |
| - | + | + | + | + | 0.44 | 0.55 | 0.42 | 0.59 | 0.90 | 0.58 |
| + | - | + | + | + | 0.35 | 0.50 | 0.32 | 0.56 | 0.81 | 0.54 |
| + | + | - | + | + | 0.48 | 0.47 | 0.32 | 0.68 | 0.90 | 0.58 |
| + | + | + | - | + | 0.21 | 0.47 | 0.27 | 0.52 | 0.62 | 0.50 |
| + | + | + | + | - | 0.06 | 0.0001 | 0.02 | 0.24 | 0.12 | 0.29 |

[a]The '+' symbol indicates the parameter for which the genotype-specific value was used, and '-' symbol indicates the parameter for which the genotype mean value was used in the model simulation. The first row (bold symbols and text) indicates the results of the baseline simulation, in which genotype-specific values were applied to all parameters.
[b]The variation explained per each experiment (number of points $n$ = 100).
[c]The variation explained for across-environment means in 100 F1 genotypes of potato (number of points $n$ = 100).
[d]The variation explained for all data points when all the observations for 100 F1 genotypes in the four experiments were pooled ($n$ = 400).

determination of tuber yield among the F1 population (Table 5.3). Li et al. (2006) also performed a similar sensitivity analysis and reported that N availability was the key trait affecting potato tuber yield. Crop N status affects photosynthesis which in turn is a function of intercepted radiation by above-ground vegetative parts (Khurana and McLaren, 1982; Moll, 1983; Marcelis et al., 1998). There is a linear relation between total N uptake and canopy growth and development until a maximum level is reached (Lemaire, 1997). The duration of the period with full canopy cover is longer and the stage of decline starts later in time the higher the N available (Chapter 2).

The sensitivity analysis gave further insight into whether or not the relative importance of the five model-input traits varies with environment. Such information about the relevance of different plant traits for yield under different growth conditions can, therefore, improve the efficiency of a breeding programme (Heuvelink et al., 2007). However, our results for experiment-specific sensitivity analysis showed that the relative importance of the five model-input traits varied little among the four experiments.

### 3.5. *Path coefficient analysis*

Path coefficient analysis was performed to understand the underlying relationships among the genotype-specific parameters and with observed tuber yield (Fig. 5.6; Table 5.4). The results revealed that parameters $N_{max}$ and $n_{SO}$ had highest significant ($P < 0.01$) positive and negative direct effects (i.e. 0.91 and -0.47, respectively) on the final tuber yield (Fig. 5.6), whereas $m_V$, $m_R$, and $H_{max}$ had least ($P > 0.05$) direct effects on final tuber yield (i.e. -0.05, -0.10, 0.00, respectively). The sum of direct and indirect effects of parameters from path coefficient analysis revealed that there existed significant ($P < 0.01$) positive effects of $m_R$, $H_{max}$, and $N_{max}$ on tuber yield (their correlation coefficients as 0.45, 0.41, and 0.81, respectively; Table 5.4).

Path coefficient analysis has been very useful in partitioning the correlation coefficient into components of direct and indirect effects and give thorough understanding of actual causal relationships and contribution of various characters on the target trait (Dewey and Lu, 1959; Samonte, 1998). Our results further indicated that relationships of parameters ($m_R$, $H_{max}$) with tuber yield were actually driven by indirect effects, mainly through $N_{max}$ (Table 5.4). These results are largely in line with our GECROS-based sensitivity analysis, suggesting that genotypes with higher $N_{max}$ may exhibit more final tuber yield provided $n_{SO}$ is low (Casa et al., 2005; Chapter 3).

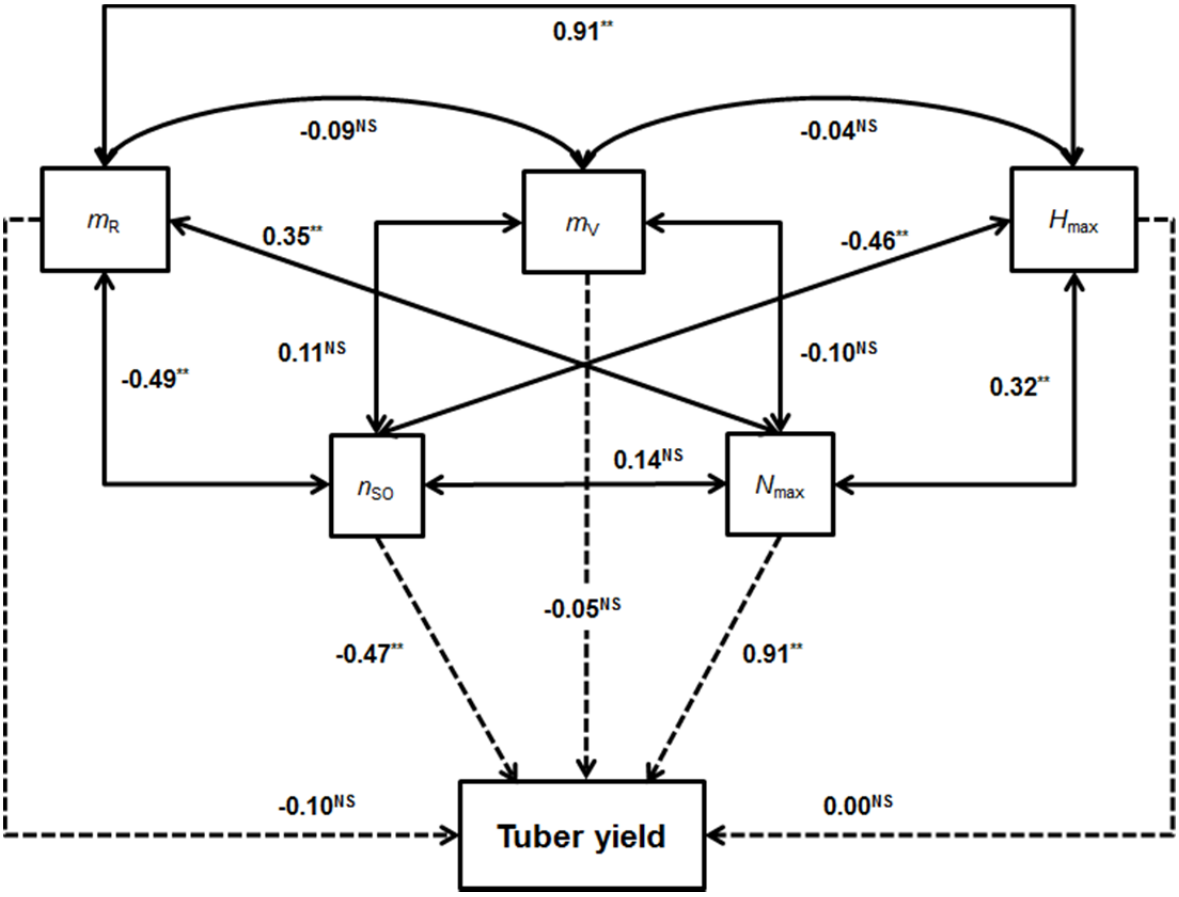


**Figure 5.6.** Path coefficient structural model describing direct and indirect effects of different genotype-specific parameters ($m_R$, $m_V$, $H_{max}$, $n_{SO}$, and $N_{max}$; see Table 5.1 for their descriptions) on the tuber yield across six experiments for an F1 population of potato. The solid line represents the correlation coefficient between two predictor variables; dashed line represents the path coefficient from the predictor variable to response variable (tuber yield). ** Significant at $P < 0.01$, NS Non-significant ($P > 0.05$).

## 4. Conclusions

Yield variation in terms of growth and development of the crop is complex, for it involves the effect of external factors on all the physiological processes, the inter-relationships between different processes and their dependence on the genetic constituent of the plant. In this study we explored the ability of the ecophysiological model 'GECROS' to analyse differences in tuber yield in a set of cultivars of maturity types and a diploid F1 segregating population. The model described well the dynamics of important growth related processes in potato and gave important insights into the underlying component traits and factors influencing the tuber dry matter production. Using five measured genotype-specific parameters ($m_V$, $m_R$, $H_{max}$,

**Table 5.4.** Path coefficient analysis of direct and indirect effects of genotype-specific parameters on the tuber yield of an F1 population of potato. *td* stands for thermal day. See Table 5.1 for parameter descriptions.

| Variable | Effect† |
|---|---|
| $m_V$ (*td* ) | |
| Direct effect | -0.052 |
| Indirect effect via | |
| $m_R$ | 0.008 |
| $H_{max}$ | 0.000 |
| $n_{SO}$ | -0.028 |
| $N_{max}$ | -0.090 |
| ***Total correlation*** | **-0.161** |
| $m_R$ (*td*) | |
| Direct effect | -0.098 |
| Indirect effect via | |
| $m_V$ | 0.004 |
| $H_{max}$ | 0.000 |
| $n_{SO}$ | 0.226 |
| $N_{max}$ | 0.318 |
| ***Total correlation*** | **0.451** |
| $H_{max}$ (m) | |
| Direct effect | 0.000 |
| Indirect effect via | |
| $m_V$ | 0.002 |
| $m_R$ | -0.089 |
| $n_{SO}$ | 0.213 |
| $N_{max}$ | 0.287 |
| ***Total correlation*** | **0.413** |
| $n_{SO}$ (g N $g^{-1}$) | |
| Direct effect | -0.473 |
| Indirect effect via | |
| $m_V$ | -0.003 |
| $m_R$ | 0.047 |
| $H_{max}$ | 0.000 |
| $N_{max}$ | 0.131 |
| ***Total correlation*** | **-0.298** |
| $N_{max}$ (g N $m^{-2}$) | |
| Direct effect | 0.908 |
| Indirect effect via | |
| $m_V$ | 0.005 |
| $m_R$ | -0.034 |
| $H_{max}$ | 0.000 |
| $n_{SO}$ | -0.068 |
| ***Total correlation*** | **0.811** |

†Across experiments

$n_{SO}$, and $N_{max}$), GECROS showed a good potential in explaining the observed yield differences among the genotypes. Simulated trends of growth were in agreement with the measured data. The model yielded reasonable predictions of differences in tuber yield across environments and across genotypes. The simulation results suggested that genotype-specific parameter $N_{max}$ contributed most to the determination of tuber yield. These results were further proved by path coefficient analysis suggesting that genotypes with higher $N_{max}$ and low $n_{SO}$ may exhibit more final tuber yield. Such information would greatly facilitate the development of ideotypes for specific environment(s).

As a whole this study highlighted the usefulness of GECROS crop growth model for exploring the impact of new genotypes and the contribution of individual physiological traits on yield by simulating the responses of genotypes across different environments. In addition, our model approach shed light on some of the mechanisms causing genotype differences in tuber yield and provided support for important aspects of hypothesis regarding N accumulation. The model analysis identified N uptake and use efficiency as possible areas for improvements in tuber dry matter production. Opportunities for improving the modelling of and understanding of N dynamics and source-sink dynamics in potato have become apparent during the study. Further analysis of the genotypic parameters should be performed in conjunction with molecular markers in order to determine their genetic control. Such information would guide research towards key processes affecting crop yields and may help orientate breeding programmes as suggested, e.g. by Yin et al. (2004); Yin and Struik (2008).

# CHAPTER 6

# General discussion

**Breeding for high-yielding genotypes: A challenge**

Breeding for high-yielding cultivars for specific and/or varied environments is a major challenge to achieve world food security in the new century. The pace at which progress has been made in achieving higher crop yields has become stagnant compared with that required by the growing demands (Cassman, 1999). The pace and efficiency of genetic progress must now increase to meet the projected demand for agricultural products (FAO, 2009).

Molecular biology has delivered commercial successes in enabling crop plants to better resist pests and tolerate herbicides and, more recently, in improving product quality. However, the challenge remains as to how to manipulate more complex growth and development traits associated with crop adaptation and yield. The inability to connect information at gene level to the expressed phenotype in a manner that is useful for selection and plant breeding has restricted adoption of molecular approaches in plant breeding (Miflin, 2000). Enhanced capabilities in genotyping have not been matched by development of enhanced capabilities in phenotyping or by development of enhanced approaches to link genotype and phenotype (Campos et al., 2004). The situation is particularly challenging for complex traits associated with crop adaptation and yield (e.g. grain or tuber dry matter or resource use efficiencies) as they are regulated by multiple interacting genes and environmental conditions, so that gene-to-phenotype relationships are not straightforward (Li et al., 2001; Luo et al., 2001). Hence, new approaches must be developed to accelerate breeding through improving genotyping and phenotyping methods and by increasing the available genetic diversity in breeding germplasm.

**Potato: A complex crop**

In potato, breeding for yield potential and range of adaptation (or degree of stability in performance over a wide range of environments) is particularly difficult due to the complexity of the crop's whole-plant physiology (cf. Van Dam et al., 1996; Celis-Gamboa et al., 2003). Growth and yield are determined by a diversity of complex crop factors including (a) the rate of leaf appearance, individual leaf growth, final leaf size, and the life span of individual leaves, (b) the number of lower and sympodial branches, (c) the overall rate of canopy development (e.g. increasing of N supply

levels accelerates crop development and the time when maximum canopy cover is reached), (d) light interception by the crop over time, (e) the rate of photosynthesis, (f) the onset of tuberisation, and (g) final tuber yield and harvest index. Furthermore, like many other complex quantitative traits, each developmental stage and crop factor in potato is likely to be regulated and controlled by a large set of interacting expressed genes throughout the plant growth and the strong influence of genotype-by-environment (G×E) interactions (Allard and Bradshaw, 1964; Jefferies and MacKerron, 1993; Bachem et al., 2000; Schittenhelm et al., 2006). All these complexities make the manipulation of yield determining traits and their prediction a challenging task in potato.

The traditional system of potato breeding is a laborious and time-consuming process, and the probability of finding superior cultivars is very low. Breeding generally involves evaluation and selection, based on many different traits including yield, disease resistance and quality, of the clonally propagated progeny of a cross between two clones. These parent clones can be existing cultivars or clones with introgression from wild species. Normally, it takes more than 10 to 15 years to produce a new cultivar (Caligari, 1992; Hunt, 1993; Haverkort and Kooman, 1997).

**Role of multi-environment trials**

Plant breeders are mostly interested in characterising genotypes in diverse environments to understand how a particular genotype performs in different environments. Individuals in genetic populations are studied in replicated experiments and distributed over 'discrete' environments which are often locations and/or years. The main task of data analysis is to estimate parameters which reveal the effects of genetic and environmental factors controlling the expression of specific traits. The parameters concerning effectiveness of selection strategies of individual genotypes, for example, are aimed to examine performance of traits and correlation between them across environments, variability of entries due to genetic and environmental components, heritability, and genetic gain over generations of selection for new superior varieties in growing regions (Tai, 2007). Information like these could help to better understand the type and size of genetic (G), environmental (E), and G×E interaction components of variation, and the reasons for their occurrence; and if necessary, a strategy to develop genotypes for particular target environments.

The G or E components of variation for any trait normally show average differences between genotypes or environments, respectively. Purely environmental effects, reflecting the different ecological potential of sites and management

conditions, are not of direct concern for the breeding or recommendation of plant varieties. However, differences between genotypes may vary widely among environments in the presence of G×E interaction effects. Therefore, there is a need to quantify the impacts of G×E in order to explore the potential opportunities towards yield improvement under the specific and/or varied environments. This could help to better understand the type and size of G, E, and G×E components of variation, and the reasons for their occurrence. It could also help to develop, if necessary, a strategy to design an ideal genotype (i.e. ideotype breeding) in potato.

In potato, however, very little systematic, quantitative information is available about genotypic differences in response to contrasting environmental conditions and/or input levels, e.g. temperature, precipitation, and nitrogen (N) fertilisation regimes. A better understanding of the physiological, genetic and environmental regulation of relationships between the main attributes of growth and yield determining components will facilitate the breeding of varieties able to perform well under specific sets of environmental conditions. In order to achieve this goal we need useful tools and more concerted efforts to understand G×E, and the benefits of integrating accumulated and expensive datasets.

**Role of crop physiology**

Besides recent developments in genomics (such as genome sequencing) that will provide useful tools and massive amounts of information to speed up the plant breeding process (Stuber et al., 1999; Miflin, 2000), an option for improving breeding efficiency is to develop and utilise a thorough understanding of underlying morphological and physiological processes that determine important traits like yield (Bindraban, 1997).

Crop physiology, as a powerful, rapidly developing and quantitative discipline, has the ability to complement plant breeding as physiological studies provide a way to dissect complex traits into simpler components that might be under separate and probably simpler genetic control (Yin et al., 2002). Any increase in yield must have a physiological basis that, if targeted, should permit a significant advance in the identification of superior genotypes (Richards, 1996). So far, however, only in a limited number of instances physiological approaches have been applied to support crop improvement programmes (Sinclair et al., 2004). This situation may change in the future if the links between physiology and genetics are established or strengthened (Miflin, 2000). There is a growing awareness that in order to better analyse phenotypes of complex traits for any crop genotype under any environmental scenario using increasingly available genomic information, integration of genetics

with quantitative crop physiology is required (Tardieu, 2003).

**Systems approaches: Their role in assisting breeding**

As highlighted in previous sections, progress in crop improvement and particularly in molecular approaches to plant breeding is limited by our ability to predict plant phenotype based on its genotype, especially for complex traits like yield (Hammer et al., 2010). New approaches could complement traditional approaches with analytical selection methodologies to further improve crop yields and the overall efficiency of the breeding process. Such new approaches will be of considerable interest to plant breeders (Chapter 1).

An important advance in crop physiology during the last four decades is the development of dynamic process-based crop growth models for predicting yields under varied environments (Boote et al., 1996). Process-based ecophysiological crop growth models have been developed by integrating knowledge across multi-disciplines such as plant physiology, ecology, agronomy, soil science, and meteorology (Loomis et al., 1979).

As quantitative crop models represent causality between component processes and yield, they can predict crop performance beyond the environments for which the model parameters were estimated. In this respect, systems approaches based on physiologically sound crop growth models can quantify and integrate crop responses to genetic, environmental, and management factors. Such an integrated approach can guide research on questions such as bridging the gap between genotype and phenotype and to potentially resolve G×E interactions (Chenu et al., 2009; Messina et al., 2009; Hammer et al., 2010; Tardieu and Tuberosa, 2010; Yin and Struik, 2010), and in proposing ideotypes for particular target environments (Hammer et al., 1999; Yin et al., 2000a, 2004; Yin and Struik, 2008). This offers a major potential of applying modelling based approaches in plant breeding strategies (Jackson et al., 1996; Chapter 1).

**Yield improvement in potato**

Tuber yield is still the most important trait to be selected for, since it remains the basis on which the grower obtains an economic return. Yield production in potato can be explained in terms of an integrated response of distinct plant physiological processes (see equation 1.1, Chapter 1). Physiological traits explaining the dynamics of canopy cover and tuber bulking are very useful as they are important determinants of yield (Hodges, 1991). The total biomass production and accumulation depend on

the intercepted photosynthetically active radiation (PAR), which is directly proportional to the crop green canopy cover (Burstall and Harris, 1983; Spitters, 1988; Tekalign and Hammes, 2005). Differences in the rate of dry matter accumulation can be attributed to differences in light interception caused by variability in growth and duration of maximum green canopy cover and its senescence, and in canopy-level efficiency of utilisation of intercepted radiation as a result of changes in the functionality of leaf photosynthesis during tuber bulking (Pashiardis, 1987; Spitters, 1988; Van Delden et al., 2001). The tuber yield is then the product of intercepted radiation and radiation use efficiency (RUE) and determined by the fraction of total biomass that is partitioned to the tubers, influenced by the rate and duration of tuber bulking (Van der Zaag and Doornbos, 1987; Spitters et al., 1989; Struik et al., 1990). All this shows that yield production in potato is the result of interactions among several crop characters which are greatly influenced by both genetic and environmental and/or management factors.

The genetic improvement of yield can be understood more mechanistically by partitioning the yield into component traits (Chapters 2 and 3) and analysing their inter-relationships (Bezant et al., 1997; Araus et al., 2008). It is a very useful approach for the breeder to split a complex trait into more simple ones, provided sufficient genetic variation exists for these traits; that they have clearly higher heritability than the complex trait, and their assessment would be easier than that of tuber yield itself.

Until now, limited efforts have been made to study the physiological and genetic basis of variability among traits determining crop performance. The key physiological and genetic processes leading to yield development and the factors affecting these processes are still not well understood. Furthermore, limited information is available on the temporal dynamics of important above- and below ground developmental processes in potato under diverse environmental conditions on a large set of contrasting genotypes. Majority of studies have focussed on one, or a very limited number of genotypes and/or cultivars. This has made more difficult the understanding of complex regulatory mechanisms underlying the dynamics of tuber formation and other developmental processes.

**Thesis approach**

Keeping in view the above discussion, this thesis aims to develop an approach to quantify and predict the temporal dynamics of yield formation of individual genotypes from a large population and to estimate parameters which could reveal the effects of genetic and environmental factors on the important plant processes controlling yield formation in potato. Besides, this study also explores the question of

whether using a crop growth and development modelling framework can link phenotypic complexity to underlying genetic systems in a way that may contribute to new insights into molecular breeding strategies as well as into possibilities to indirectly select for higher yield. We approach this question by physiological dissection and integrative modelling of complex traits in potato. Figures 1.2-1.3 (Chapter 1), present a schematic representation of the overall approach employed in this thesis. Like most genetic studies in potato, we chose a diploid ($2n = 2x = 24$) F1 segregating population (i.e. SH × RH) in order to avoid the complexity of tetrasomic inheritance (Bradshaw and Mackay, 1994; Meyer et al., 1998). This population is well adapted to the growing conditions of the Netherlands and segregates for maturity (Van der Wal et al. 1978; Van Oijen 1991). Besides, we also used five standard cultivars with very different maturity types (i.e. Première, Bintje, Seresta, Astarte, and Karnico) as standard genotypes. The data sets used in thesis are primarily based on six contrasting field experiments carried out in Wageningen (52° N latitude), the Netherlands, during 2002, 2004, and 2005. These experiments differed in environmental conditions because they were carried out in different years, on different soils and under different N fertiliser regimes, thereby creating six contrasting environments. For more details about the plant material used and experimental details (see Materials and methods, Chapter 2).

In the following sections, I discuss the main findings and overall contribution of this thesis.

***An approach for analysing the dynamics of canopy cover and tuber bulking***

As mentioned in the previous section, intercepted radiation has been found to be linearly correlated with the quantity of dry matter produced which, in the case of potatoes, depends on the leaf canopy size, rate, and the duration over the growing season to intercept radiant energy (Van der Zaag, 1984; MacKerron and Waister, 1985a,b; Van der Zaag and Doornbos, 1987; Fahem and Haverkort, 1988; Van Delden et al., 2001). Tuber bulking in potato, on the other hand is the determinant process in the formation of harvestable products of potato crop. It marks the onset of the production phase of the potato crop after a dynamic sequence of several complex physiological events (Ewing and Struik, 1992; Jackson, 1999; Struik et al., 2005). Quantitative understanding of both canopy and tuber bulking dynamics is therefore imperative to explain potato production under particular conditions.

Research has addressed many aspects of potato canopy growth and development (e.g. Fleisher and Timlin, 2006; Fleisher et al., 2006; Vos and Biemond, 1992); however, insights into the relationships among environment, nutritional, and

other factors, particularly with respect to canopy cover and its relation with whole-plant physiology are still lacking (Almekinders and Struik, 1996). Despite the importance of potato tubers as a source of food and a means of propagation, the initiation, growth and development of tubers and the factors affecting these processes are not well understood, especially in the context of large number of contrasting genotypes and diverse multi-environments under field conditions. Until now, few studies have quantitatively and systematically explored the temporal dynamics of tuber bulking for a wide range of genotypes, with the exception of the work by Spitters (1988) and Celis-Gamboa et al. (2003).

In Chapter 2, we therefore developed a quantitative approach to break down the time course of canopy cover during the entire crop cycle as a function of thermal time into component traits. Canopy cover development pattern was subdivided into distinct stages using a beta function based on Yin et al. (2003, 2009). The model (eqns 2.1-2.3, Chapter 2) describes three phases of canopy development (i.e. canopy build-up phase, maximum cover phase, and canopy decline phase) through multiple parameters defining the timing, rate, duration and area under green canopy curve ((see Fig. 2.1 in Chapter 2); Table 6.1). These traits were biologically meaningful and directly related to the ability of the adapted genotypes to intercept PAR and thus to create high tuber yields. Many of these traits showed significant genetic variation.

In addition, Chapter 3 presents a quantitative approach to analyse the dynamics of tuber bulking during the entire crop cycle and its variability among a large set of potato genotypes and to break the time course and its variation down into biologically meaningful and genetically relevant component traits. Tuber bulking results from two basic processes, tuber initiation and tuber growth. Tuber growth normally follows a sigmoid pattern as a function of time, including an early accelerating phase, a linear phase, and a maturation phase (see Fig. 3.1 in Chapter 3). These processes can be described by using the expolinear function of Goudriaan and Monteith (1990) as described by eqn 3.1 (Chapter 3). However, because of its curvilinear nature the true growth rate in the linear phase is under-estimated. We therefore modified the approach of Goudriaan and Monteith (1990) and quantified these phases together with a piece-wise expolinear function (i.e. combined eqns 3.1-3.3; Chapter 3). Several parameters were generated describing the rate and duration of linear phase of tuber bulking (Table 6.1).

To account for the influence of daily and seasonal temperature fluctuations on tuber growth, all time variables and duration were expressed as thermal days (*td*) following our approach in Chapter 2. According to the results, our model approach successfully described the sigmoidal time-course curve of canopy growth (Fig. 2.2, Chapter 2) and the dynamics of tuber bulking (Fig. 3.2, Chapter 3) of individual

genotypes from a large set of population across varied environments via agronomically meaningful traits (as discussed later).

***Quantification of resource use efficiencies***

Productivity increase can also be accompanied by an increase in the genotype's resource use efficiency. Efficient utilisation requires both effective capture of resources and efficient conversion into useable biomass. In potato, plant growth including canopy production for efficient light interception and photosynthesis (see earlier text) depends on adequate nutrition, and optimised fertiliser inputs, especially N. Both radiation and N are therefore essential resources for efficient crop production. The variation in dry matter content among cultivars can also partly be attributed to the variation in efficiency of diverting of more dry matter to the tubers (Spitters, 1988; Struik et al., 1990). Therefore the interpretation of plant growth in terms of accumulated intercepted PAR, N uptake and the efficiency with which these resources are used for dry matter production should receive adequate attention in potato breeding programmes.

The aim of this thesis was also to produce tools and materials suitable for breeding new crop varieties with improved resource (i.e. radiation and N) use efficiencies and to study how they are influenced by genetic and environmental influences. Nonetheless, interventions in breeding based on understanding of the genetic and physiological basis of crop performance have the potential to accelerate genetic gains for yield and resource use efficiencies. We therefore analysed radiation- and N use efficiencies (RUE and NUE, respectively), and their relationships with our estimated physiological model traits.

The term RUE refers to the slope of the relation between total dry matter (g $m^{-2}$) and cumulative intercepted radiation (MJ $m^{-2}$) (Haverkort and Harris, 1987). Similarly, NUE is generally defined as the ratio between total plant dry weight and plant N uptake. In this thesis, however, due to lack of detailed measurements of total plant biomass for our large set of genotypes, radiation and N use efficiencies were estimated on the basis of tuber-dry weight for each individual genotype/cultivar by dividing the total tuber dry matter at maturity (g DM $m^{-2}$) by the cumulative intercepted PAR (MJ $PAR_{int}$ $m^{-2}$) and total tuber N uptake (g N $m^{-2}$), respectively (Chapter 3).

The results indicated that there existed a significant ($P$<0.01) wide variation for both RUE and NUE within the F1 population with values ranging from 1.5 g DM $MJ^{-1}$ to 2.6 g DM $MJ^{-1}$ and 54.4 g DM $g^{-1}$ N to 81.6 g DM $g^{-1}$ N, respectively (Table 3.2, Chapter 3). These wide variations (see Fig. 3.3, Chapter 3) suggested transgressive

**Table 6.1.** Description of parameters reproduced from Chapters 2 and 3. *td* stands for thermal day.

| Trait | Description | Unit |
|---|---|---|
| ***Canopy cover dynamics*** | | |
| $t_{m1}$ | Inflexion point during canopy build-up phase | *td* |
| $t_1$, $D_{P1}$ | Period from plant emergence to maximum canopy cover (moment and duration since emergence, respectively) | *td* |
| $t_2$ | Onset of canopy cover senescence | *td* |
| $t_e$ | Time of complete senescence of canopy cover or crop | *td* |
| $v_{max}$ | Maximum level of canopy cover | % |
| $c_{m1}$ | Maximum canopy growth rate during build-up phase | % $td^{-1}$ |
| $c_1$ | Average canopy growth rate during build-up phase | % $td^{-1}$ |
| $c_3$ | Average canopy senescence rate during decline- phase | % $td^{-1}$ |
| $D_{P2}$ | Total duration of maximum canopy cover phase | *td* |
| $D_{P3}$ | Total duration of canopy senescence phase | *td* |
| $A_1$ | Area under canopy curve for $D_{P1}$ | *td %* |
| $A_2$ | Area under canopy curve for $D_{P2}$ | *td %* |
| $A_3$ | Area under canopy curve for $D_{P3}$ | *td %* |
| $A_{sum}$ | Area under whole green canopy curve | *td %* |
| ***Tuber growth*** | | |
| $t_B$ | Onset of linear phase of tuber bulking | *td* |
| $t_E$ | End of linear phase of tuber bulking | *td* |
| *ED* | Total duration of tuber bulking | *td* |
| $c_m$ | Rate of tuber bulking | g $td^{-1}$ |
| $w_{max}$ | Maximum tuber dry matter at crop maturity | g $m^{-2}$ |

segregation.

The continuous selection in most breeding programmes has very much narrowed down the genetic base for important resource use efficiencies in most modern day potato cultivars (Brown, 1993; Love, 1999). This thesis concluded that there are enough possibilities to exploit the available variation in the SH × RH breeding population and may offer more efficient screening possibilities for

improving resource (radiation and N) use efficiencies. In the coming sections we will discuss the basis of this variation.

***Genetic analysis***

The prospects of improving a target trait by selecting for component traits is mostly determined by their correlation with the target trait (e.g. yield) as well as amount of heritable or genetic variation for the particular component traits relative to that of non-heritable or environmental variation, and by the nature and magnitude of G×E interaction. Therefore, an understanding of such relationships within potato germplasm is important to establish a broad genetic base for breeding purposes.

Results of the current thesis demonstrated that standard cultivars exhibited significant ($P$<0.05) differences with respect to component traits controlling the dynamics of canopy cover and tuber bulking, resource (radiation, N) use efficiencies, and final tuber yield. Not surprisingly, in most cases, performance of the commercial potato cultivars was superior to that of the diploid F1 population (Tables 2.2; 3.1-3.2). Tetraploid potatoes are typically more vigorous and high yielding (DeMaine, 1984; Hutton, 1994). The somewhat decreased vigour and yield in diploids may be due to their ploidy reduction and inbreeding depression (Kotch, 1987).

Estimates of different components of variance can be used to formulate the most efficient breeding strategy for improved genotypes. Study of sources of variation among the tested F1 genotypes indicated that there was significant ($P$<0.01) genetic variation for most traits determining the course of canopy development, tuber bulking, and (radiation, N) resource use efficiencies (Chapters 2 and 3).

The results further indicated that some genotypes performed best across the environments. Table 6.2 presents the means of top 10% of the out-performing F1 genotypes for few selected physiological traits. Such genotypes could be very useful for selection and further testing in breeding programmes.

Heritability of a trait is a key component in determining genetic advance from selection (Nyquist, 1991). The results indicated high broad-sense heritability ($H^2$) estimates across environments for most traits. For instance, >80% $H^2$ values were recorded for traits ($t_2$, $t_e$, $D_{P2}$, $A_2$, $A_{sum}$, $c_m$, $t_E$, $ED$, RUE, and NUE) (cf. Tables 2.6 (Chapter 2) and 3.5 (Chapter 3)). These results suggested that these are repeatable traits and strongly expressed across a range of environmental conditions. On the other hand low broad-sense heritability as well as minimum $CV_G$ estimates for $t_1$ or $D_{P1}$ and $c_3$ indicated that total duration of canopy build-up phase and rate of canopy senescence, respectively is sensitive to the environment (mainly N) (Table 2.4, Chapter 2).

Table 6.2. List of top ten best performing F1 genotypes for specific physiological model traits. Trait values indicate genotype mean across environments. For description of traits see Table 6.1. * denotes particular genotypes that performed well in low N environment (i.e. Exp 3).

| No. | Genotype | $t_e$ (*td*) | Genotype | $D_{P2}$ (*td*) | Genotype | $A_{sum}$ (*td %*) | Genotype | $c_m$ (g $td^{-1}$) |
|---|---|---|---|---|---|---|---|---|
| 1 | SHRH83-L9* | 79.5 | SHRH83-L9 | 32.6 | SHRH34-H6* | 6146.4 | SHRH11-F10* | 61.6 |
| 2 | SHRH34-H6* | 79.3 | SHRH-136 | 32.4 | SHRH83-L9* | 5836 | SHRH53-J8* | 58.1 |
| 3 | SHRH-136* | 75.4 | SHRH-150 | 28.3 | SHRH-136* | 5739.3 | SHRH118-C7* | 53.5 |
| 4 | SHRH29-H2 | 73.1 | SHRH-148 | 27.5 | SHRH-148 | 5156.9 | SHRH51-J7* | 53.5 |
| 5 | SHRH-148 | 73.0 | SHRH73-B11 | 27.1 | SHRH67-K9* | 5092.7 | SHRH-465 | 53.0 |
| 6 | SHRH9-F8 | 71.2 | SHRH-428 | 26.1 | SHRH29-H2 | 5065.6 | SHRH86-L12* | 52.0 |
| 7 | SHRH73-B11 | 71.0 | SHRH71-K12 | 25.5 | SHRH9-F8 | 5061.0 | SHRH17-G5* | 50.8 |
| 8 | SHRH67-K9* | 71.0 | SHRH179-E5 | 24.7 | SHRH73-B11 | 5022.4 | SHRH138-C10* | 50.4 |
| 9 | SHRH111-N12 | 70.6 | SHRH9-F8 | 24.5 | SHRH-150 | 4992.2 | SHRH-500* | 50.3 |
| 10 | SHRH179-E5 | 70.1 | SHRH89-M3 | 24.3 | SHRH179-E5 | 4984.6 | SHRH35-H7 | 48.8 |

| No. | Genotype | *ED* (*td*) | Genotype | RUE (g DM $MJ^{-1}$) | Genotype | NUE (g DM $g^{-1}$ N) | Genotype | $w_{max}$ (g $m^{-2}$) |
|---|---|---|---|---|---|---|---|---|
| 1 | SHRH83-L9 | 68.0 | SHRH-477* | 2.78 | SHRH-136* | 78.7 | SHRH42-H12* | 1215.9 |
| 2 | SHRH-136 | 66.4 | SHRH11-F10 | 2.77 | SHRH-406* | 78.2 | SHRH-406* | 1177.9 |
| 3 | SHRH34-H6 | 63.1 | SHRH33-H5* | 2.77 | SHRH71-K12* | 78.1 | SHRH11-F10 | 1166.2 |
| 4 | SHRH29-H2 | 60.8 | SHRH23-G9* | 2.64 | SHRH114-O3* | 77.5 | SHRH53-J8* | 1163.8 |
| 5 | SHRH67-K9 | 60.3 | SHRH-500 | 2.61 | SHRH34-H6* | 77.3 | SHRH34-H6 | 1158.0 |
| 6 | SHRH9-F8 | 58.0 | SHRH35-H7* | 2.59 | SHRH-148* | 76.4 | SHRH179-E5 | 1122.0 |
| 7 | SHRH-416 | 56.5 | SHRH97-M9* | 2.56 | SHRH17-G5* | 74.8 | SHRH89-M3* | 1116.1 |
| 8 | SHRH87-M1 | 54.2 | SHRH95-M7* | 2.55 | SHRH67-K9* | 74.2 | SHRH6-F5 | 1115.8 |
| 9 | SHRH71-K12 | 53.2 | SHRH-465* | 2.55 | SHRH-150* | 73.8 | SHRH97-M9 | 1107.3 |
| 10 | SHRH179-E5 | 51.7 | SHRH53-J8 | 2.47 | SHRH-478* | 73.3 | SHRH83-L9* | 1094.0 |

G×E interaction is an extremely important issue in potato breeding as such interaction impedes plant breeding progress for complex traits such as yield and is considered to be among the major factors limiting response to selection (Tarn et al., 1992; Bradshaw, 1994; Kang, 1998). The development of shoots and tubers in potato is strongly influenced by both genetic and environmental factors. In this study, it was noted that proportion of G×E interaction variance was greater than the G variance component for traits determining the canopy build-up and senescence phases, see Fig. 2.2 (Chapter 2). These traits mainly included maximum canopy cover ($v_{max}$), rates of canopy growth and senescence ($c_{m1}$, $c_1$, and $c_3$), duration ($D_{P1}$) and area under canopy cover ($A_1$) when canopy cover reaches its maximum, duration ($D_{P3}$) and area under canopy cover ($A_3$) of canopy senescence (Table 2.3, Chapter 2). This could mean that these traits may show a range of phenotypic expressions when subject to diverse environments due to G×E interaction. The larger the G×E interaction component, the smaller the heritability estimate; thus, selection progress would be reduced as well. However, the moderate ($50\% < H^2 \leq 70\%$) heritability estimates for most of these traits indicated that these traits are responsive to selection (Table 2.6, Chapter 2).

Our results further indicated that some important physiological traits were stable across the environments on account of their G component of variance being higher than the G×E interaction. These traits included onset of canopy senescence ($t_2$), crop maturity ($t_e$), duration ($D_{P2}$) and area under canopy cover ($A_2$), when canopy cover is at maximum level (or 100%), and total area under green canopy cover ($A_{sum}$) (Table 2.3, Chapter 2).

In case of traits related to the dynamics of tuber bulking and resource (radiation and N) use efficiencies, the nature of the data sets (i.e. lack of independent replication of estimations) did not allow estimating the G×E component of variation for these traits. However, high $CV_G$ estimates for these traits along with high (>80%) broad-sense $H^2$ (as discussed earlier) indicated strong genetic basis for these traits (Table 3.5, Chapter 3).

Study of sources of variation for tuber yield *per se* on the other hand, indicated high contribution of environmental (E) variance in its total observed phenotypic variance (Table 3.4, Chapter 3). This is not surprising as yield is a complex trait and the net result of many plant physiological processes and their relationships with the environment particularly N as discussed in the later sections.

For a successful breeding programme, genetic diversity and variability in a population plays a vital role (Omoigui et al., 2006). This thesis clearly indicated that there exists strong genetic diversity in the SH×RH germplasm for nearly all the model traits. There are opportunities to further analyse and exploit this wide genetic variability available, which could potentially be used in breeding programmes aimed

at improving canopy, as well as tuber bulking dynamics and resource (radiation, N) use efficiencies and ultimately tuber dry matter production.

***Role of environment***

Plant breeders are mostly interested in characterising genotypes in diverse environments to understand how a particular set of genotypes perform differently in different environments. A thorough understanding of the relationship between the crop and the environment may help to increase potato productivity for specific environments.

In this thesis, environment represents a combination of year, site, and different N availability regimes (Chapter 2). Typically, N is the key environmental variable affecting the important yield determining growth and development processes of potato (Honeycutt et al., 1996). N management is therefore a high priority in potato cropping systems. In this study we lacked precise information about amount of mineral N becoming available during the course of crop growth. However, crop N uptake can be used as a site-specific indicator of N that is "available" to the crop (Sullivan et al., 2008). Therefore, to assess the role of N, total amount of N uptake by tubers was used as an indicator of N availability per each environment (Table 2.1, Chapter 2).

Our results further indicated good correlations among the environments for most of physiological traits, e.g. $A_{sum}$. However, the correlations varied much for some traits like $t_1$ or $v_{max}$. It is obvious that traits more sensitive to environment and/or G×E interaction show more heterogeneity among the environments (Fig. 6.1). Ranking of genotypes changed across the environments (Table 6.2) with maximum variability observed within the F1 population under low N environment (i.e. Exp 3) (Table 2.1, Figs. 2.3-2.4 (Chapter 2); Table 3.4 (Chapter 3)). Such changes in genotype ranking have been defined as cross-over G×E interactions (Baker, 1988). Cross-over types of interactions are important to breeders and production agronomists for identifying adapted traits and may enable selection strategies for developing improved varieties.

Plant breeders and geneticists have a long-standing interest in investigating and integrating G and G×E interaction in selecting superior genotypes for specific applications and for particular target environments with highest possible economical yield and resource use efficiencies (Kang and Pham, 1991). It was remarkable to note that some genotypes - besides performing best in N sufficient environments – were also highly ranked under resource poor conditions (i.e. Exp 3 with low N availability).

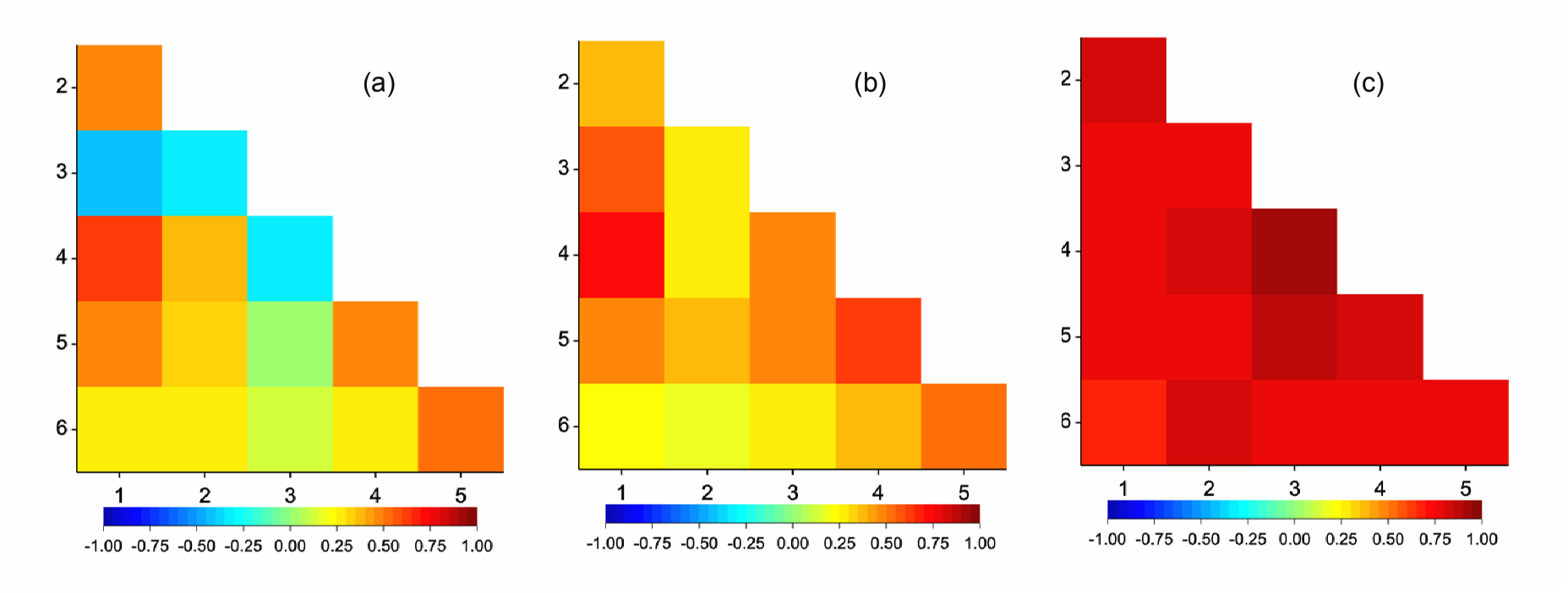


**Figure 6.1.** Heat maps revealing correlations between six environments for traits (a) $t_1$ (b) $v_{max}$, and (c) $A_{sum}$ within F1 population of potato. For description of traits see Table 6.1.

Table 6.2 indicates such genotypes for few selected physiological model traits. For instance genotypes SHRH34-H6 and SHRH-136 showed maximum values for $t_e$ (time of crop maturity), $A_{sum}$ (area under whole green canopy curve) whereas some other genotypes (e.g. SHRH11-F10, SHRH53-J8) indicated high $c_m$ (rates of tuber bulking). It was further noted that the majority of best performing genotypes indicated high resource (radiation and N) use efficiencies under low N environment (Chapter 3; Table 6.2). Moreover, some of the best yielding genotypes also yielded relatively very well under low N conditions (e.g. SHRH42-H12, SHRH-406, SHRH53-J8, and SHRH83-L9; Table 6.2). Such genotypes therefore could be very useful for breeding for widely adapted potato lines.

In addition, focus on why particular genotypes perform exceptionally well in low or high input situations could enable selection strategies to be developed for improved varieties.

Overall, these results indicate that N availability might be one of the key driving factors for causing trade-offs between the physiological traits in different environments. Moreover, results suggested that N availability and its interaction with genotype's maturity type mainly contribute to the G×E interaction of the growth and development related processes in potato (see Fig. 3.5, Chapter 3). This thesis therefore allowed a partial understanding of the environmental causes of the observed G×E interactions.

***Understanding maturity in potato***

Crops undergo sequential developmental phases from emergence to senescence that are not only characterised by their chronological age, but also by their phenology and reproductive capacity. In most annual crop plants, the transition to the maturity is marked by the onset of flowering and seed production (Bond, 2000). However, in the case of potato, progress to maturity is difficult to assess. This is mainly because most potato genotypes possess indeterminate growth pattern and therefore maintain the capacity to develop new leaves and continue to grow throughout the major part of their life cycle (Struik and Ewing, 1995; Almekinders and Struik, 1996; Fleisher et al., 2006).

The sequential phases of growth determining the duration of phenological stages of potato genotypes could be used to define the maturity type of genotype(s). In order to better understand the maturity type in potato and to study the consequences of maturity type on the canopy cover and tuber bulking dynamics as well as resource (radiation, N) use efficiencies, a set of cultivars covering a wide range of maturity types were included in this thesis, see Material and Methods (Chapter 2).

The results indicated that length of the canopy build-up phase ($t_1$ or $D_{P1}$) was conservative. Genotypic differences during early growth stages of potato are less distinct (Spitters, 1988). The duration of maximum canopy cover ($D_{P2}$) and the canopy decline phase ($D_{P3}$) varied greatly with maturity type, with late maturing genotypes having longer $D_{P2}$ and $D_{P3}$ and thus accumulated higher area under whole green canopy curve ($A_{sum}$) (Table 2.2, Chapter 2). The amount of light intercepted is in proportion to the area under the whole green canopy curve (Vos, 1995a; Fig. 6.2).

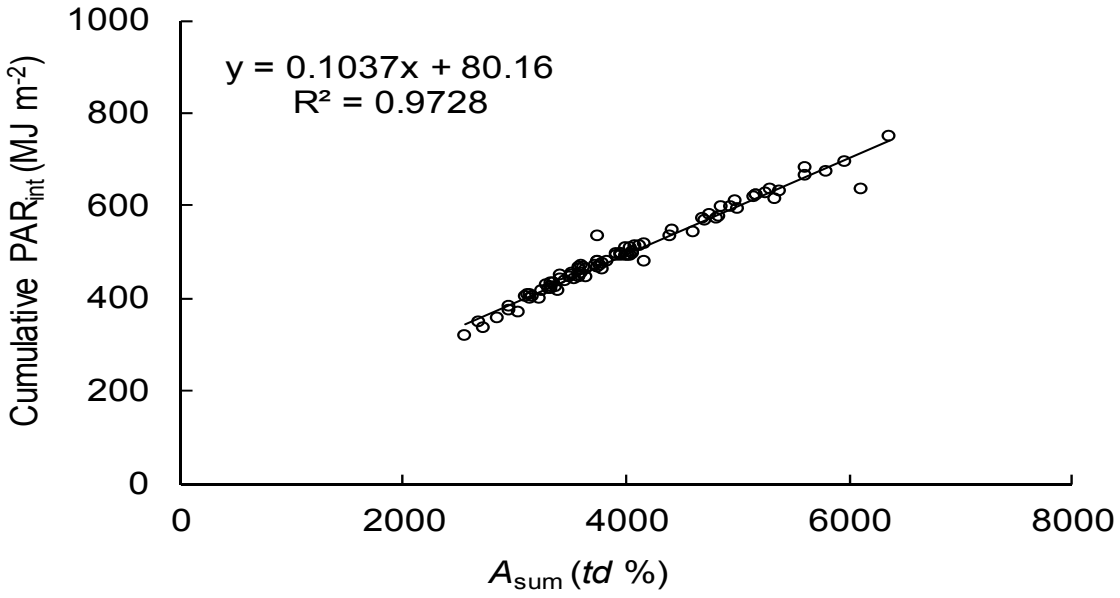


**Figure 6.2.** Relationship between cumulated PAR interception and area under whole green canopy curve ($A_{sum}$) in an F1 population of potato across environments.

The tuber bulking rate ($c_m$) was highest for early maturing genotypes followed by mid-late and then late genotypes. Late maturing genotypes had longest period of tuber bulking ($ED$) followed by mid-late and early genotypes. As a result crop matured ($t_E$) later and tuber yield ($w_{max}$) was higher in late genotypes than in early genotypes (Table 3.1, Chapter 3). This was in line with Kooman and Rabbinge (1996) and Spitters (1988), who reported that, compared with late cultivars, early potato cultivars allocate a larger part of the available assimilates to the tubers early in the growing season, resulting in shorter growing periods and also lower yields. On the other hand, late maturing cultivars combine a long canopy cover with a long tuber bulking period ($ED$) and therefore achieve more tuber dry matter yield ($w_{max}$) per

unit of N uptake than mid-early and early maturing cultivars (Zebarth et al., 2008). Figure 6.3 illustrates the relationship between crop maturity and final tuber yield for a set of standard cultivars and (SH × RH) segregating population.

The results were further evaluated for relationship between maturity and resource (radiation, N) use efficiencies. RUE values were highest for early maturing genotypes followed by mid-late and late genotypes (Table 3.1, Chapter 3). This might be related with the leaf age, which is linked with the partitioning of dry matter. If the foliage of a crop remains green for a longer period, for example in late-maturing cultivars, and no new leaves are formed in the late part of the growing season, the leaves can become so old that the rate of photosynthesis declines towards the end of the season resulting into low RUE values (Van der Zaag and Doornbos, 1987). In contrary, results indicated high NUE estimates for potato cultivars with later maturity (Zebarth et al., 2003, 2004). The reduced canopy senescence and greater partitioning of N to above ground parts most likely contributed to the high measured values of NUE for late cultivars (Sharifi et al., 2005).

This thesis indicated that most of the physiological model traits (either individually or in combination) elaborately explained the genetic variation in maturity type. Our approach could be useful in elucidating the role of maturity type in potato.

The definition of maturity type as a genotypic trait in potato, however, is rather ambiguous and currently there are so many unclear interpretations. Many public and private institutions have tried to define the maturity type in potato and have come up with their own definitions. The conventional method or criterion of elucidating the maturity type used is mostly based on visual observations made in the field at particular time intervals during the crop cycle and transferring that information to unit-less ordinal scales. This criterion does not have any biological meaning and involves ambiguity and much speculation in understanding the background of maturity, partly because of the different viewpoints of growers and processors. The added physiological and quantitative knowledge gained in Chapters 2 and 3 were therefore used to evaluate the conventional system of maturity type and to quantify and re-define the concept of maturity type on physiological basis for a large set of genotypes. Four traits ($D_{P2}$, $c_m$, $ED$, and $A_{sum}$,) were selected among the large set of physiological traits based on their high direct response to selection (Table 6.3), a re-defined physiological based maturity criteria was developed and compared with the conventionally used criterion (Chapter 4). The results indicated that the conventional-criterion based maturity scores showed more chances of errors and lack of repeatability in maturity scoring throughout the different maturity classes (very early, early/mid-early, mid-late/late, and very late). Moreover, the method of

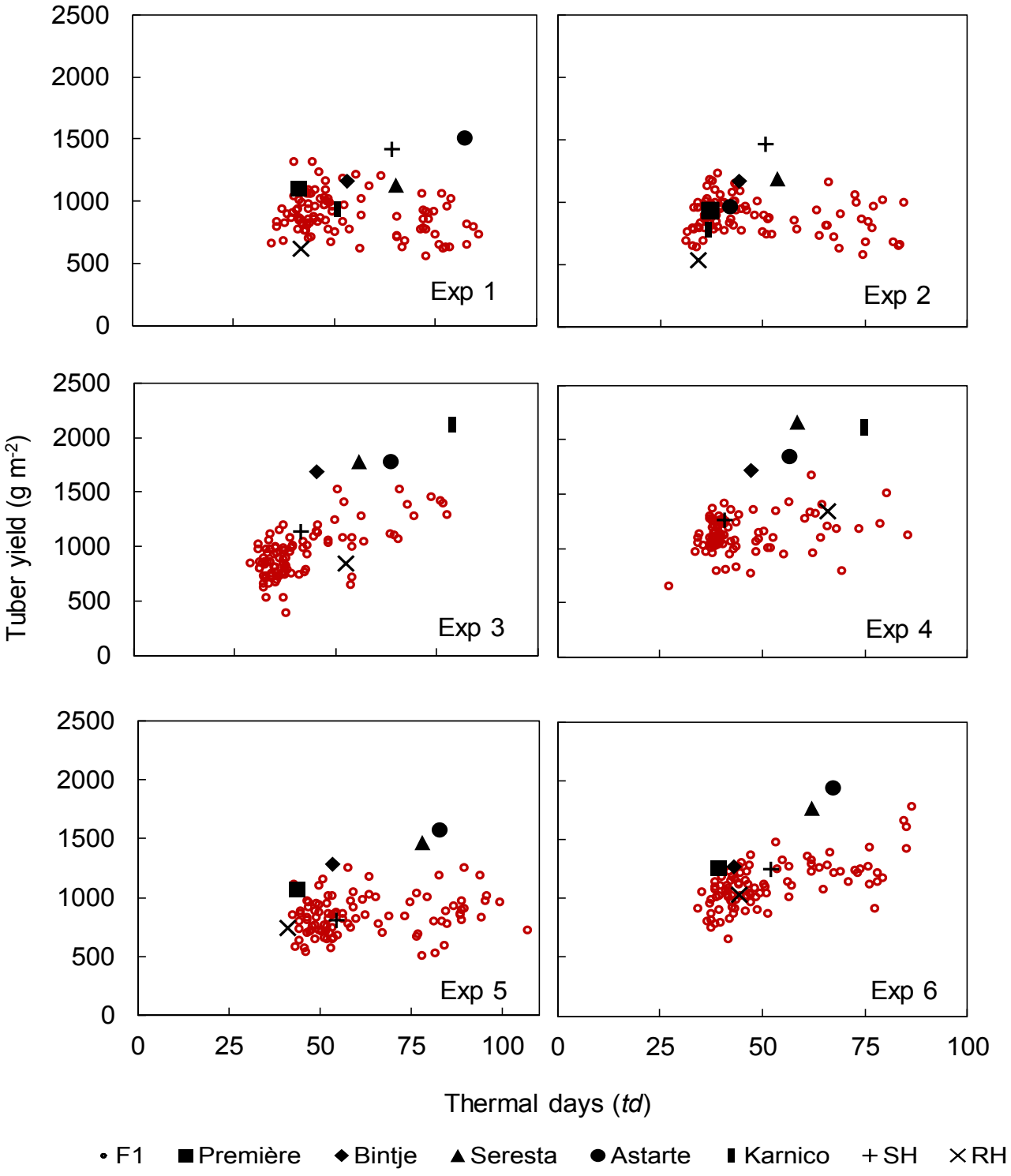


**Figure 6.3.** Final tuber yields of 100 F1 genotypes, 5 standard cultivars, and 2 parental genotypes (SH and RH), measured in each individual experiment.

classification lacked the capability to clearly interpret and discriminate between maturity classes for the crucial growth related processes of potato (e.g. $A_{sum}$) (see Fig. 4.5, Chapter 4).

The re-defined criteria of maturity type based on physiological traits on the other hand tended to define maturity classes less ambiguously and with a clear conceptual basis. This study therefore indicated that re-defining the maturity type of a large set of genotypes is possible on the basis of physiological traits and may prove very useful.

The physiological traits related to the capability of genotype to intercept PAR and its rate and duration of tuber bulking were indicated crucial for maturity and therefore could be used to quantify variation in maturity type among sets of new, unknown potato genotypes (Chapter 4).

The new physiology-based maturity definition would not only allow relating the maturity to crop phenology and physiology but could also offer wider applications in potato breeding and crop management studies. One such application would be to help in designing breeding strategies for potato ideotypes with specific maturity type for specific growing conditions and/or environments.

***Inter-relationships among the physiological traits***

Yield is a complex trait associated with many inter-related components (Yan and Wallace, 1995). The knowledge of quantitative relationships among physiological characters determining yield can provide useful insights into how differences of the complex trait and the significance in correlations between component and complex traits (e.g. yield) come about (Chapter 1). In addition, determining the physiological traits most involved in the formation of a yield component could give insight into the possibilities of manipulating the size or number of the component.

Although information about the correlation of agronomic and morphological characters with yields is helpful in the identification of the components of this complex character, yet these do not provide precise information on the relative importance of direct and indirect influences of each of the component characters. Many researchers (e.g. Bhatt, 1972) have reported that merely correlation studies do not clearly reveal such type of information and can be misleading if the high correlation between two traits is a consequence of the indirect effect of the traits (Dewey and Lu, 1959). Procedures like path coefficient analysis permit a thorough understanding of relationships and contribution of various characters to the target trait by partitioning the correlation coefficient into components of direct and indirect effects.

Path coefficient analysis was therefore performed to quantify the inter-relationships of our physiological model traits and to indicate whether their influence is directly reflected in the tuber yield ($w_{max}$) or if they take some other pathways to produce an effect. The results revealed that traits like $A_{sum}$ followed by RUE and $c_m$ exerted the highest direct influence on $w_{max}$ (Table 3.7; Fig. 3.6, Chapter 3).

The results indicated that high direct effects of $A_{sum}$ on $w_{max}$ were mainly due to significant ($P$<0.05), strong positive phenotypic correlations between $A_{sum}$, *ED*, and NUE (Fig. 3.6, Chapter 3). On the other hand significant, strong, positive phenotypic correlations ($r$ = 0.69) between RUE and $c_m$ were reflected in their higher values of direct effect on $w_{max}$. However, results indicated that total effects (i.e. sum of direct and indirect effects) of traits $c_m$ and RUE on $w_{max}$ were reduced mainly due to the strong, negative, indirect effects of $A_{sum}$ on these traits (Table 3.7, Chapter 3). The results further indicated that effects of traits *ED* and NUE on the tuber yield consisted mostly of positive indirect influences mainly through $A_{sum}$, suggesting a correlated response in selection (Table 3.7, Chapter 3).

These findings therefore suggested that selection for $A_{sum}$, RUE, and $c_m$ should be emphasised in breeding programmes for improving tuber yields. Donald (1968) proposed that an ideal genotype is that with a specific combination of characteristics favourable for growth and yield production based on the knowledge of plant and crop physiology and morphology. Our results further indicated that an ideal potato genotype from a breeding perspective is characterised by green canopy cover that intercepts solar radiation for as long as possible (i.e. with higher $A_{sum}$) during the available growing season to accumulate as much dry matter as possible maintaining a maximum capacity to divert dry matter to the tubers (i.e. with greater period of tuber bulking (*ED*)) without compromising the optimal levels of growth rates ($c_m$) and RUE ensuring highest possible economical tuber yields. Figure 6.4 schematically highlights various situations of potato ideotypes under both optimum and resource poor (low N) conditions. Researchers could then strive to obtain an optimum combination of yield components that would best suit the requirement for high yielding ability in potato genotypes for any particular environment.

***Indirect selection for yield in potato***

In a traditional crop breeding programme, elite lines are inter-crossed and then the highest yielding lines are selected. However, yield selection is empirical due to low heritability and a high genotype–environment interaction (Reynolds et al., 1999). It also requires the evaluation of a large number of advanced lines in field yield trials

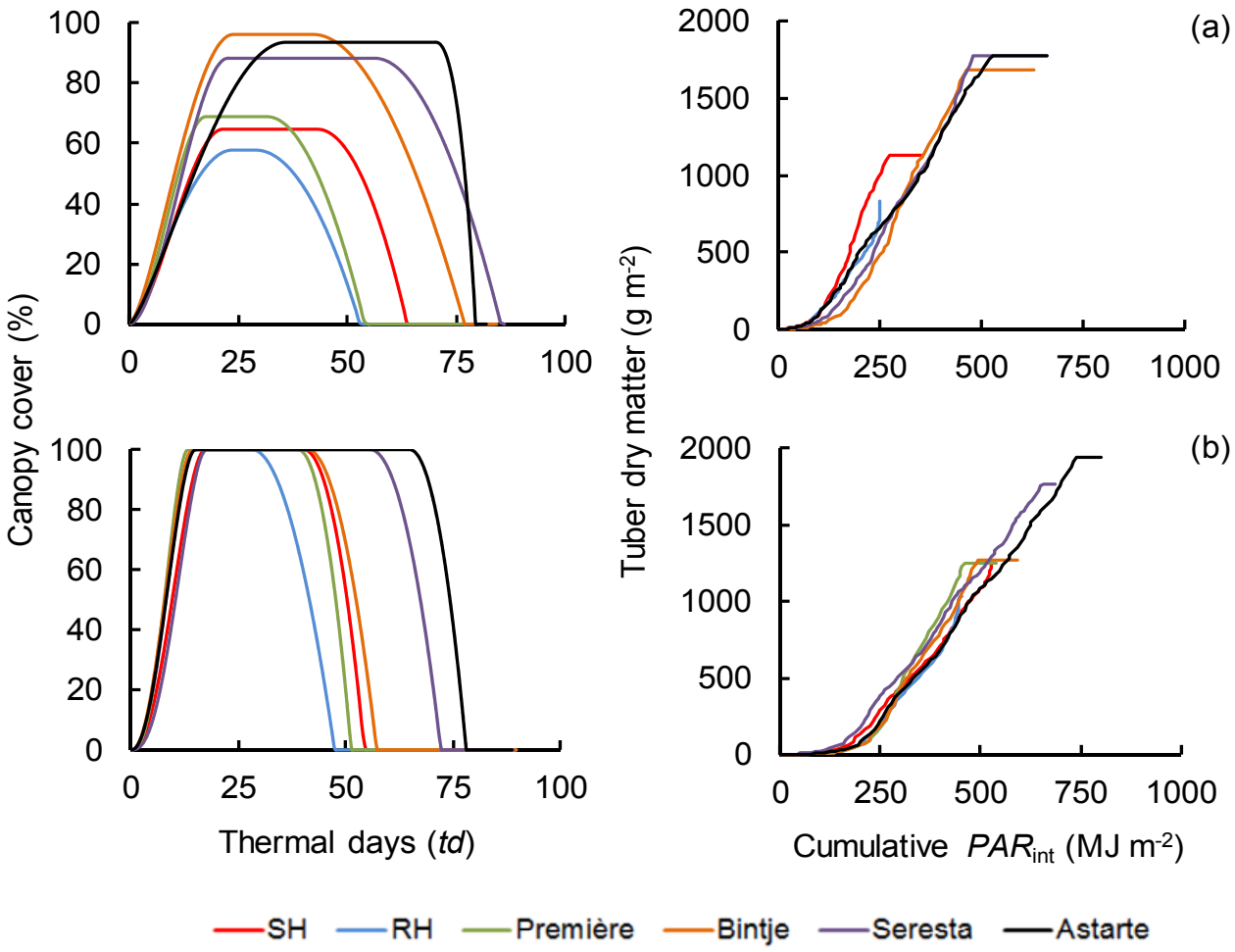


**Figure 6.4**. Schematic representation of the course of green canopy cover and tuber dry matter production of 5 standard cultivars, and 2 parental genotypes (SH and RH) for (a) low N situation (Exp 3) and (b) optimum N situation (Exp 6).

over several years and locations (Ball and Konzak, 1993). Potato breeding programmes therefore constantly need new strategies to improve efficiency by increasing the frequency of selected genotypes and reducing time and costs.

An alternative strategy that gives a high indirect response to selection for average yield over the production environments has the potential for screening large numbers of genotypes in breeding programmes for identifying and selecting high-yielding lines (Shorter et al., 1991; Cooper et al., 1995; Marti et al., 2007). In this context, the best approach would be to select for component traits that are putatively related with a higher yield potential and/or to the improved behaviour of the crop when grown in a particular environment. This is known as *analytical* or *physiological*

breeding (Chapter 1).

One of the key objectives of this thesis was to identify physiological traits which could be useful as a selection criterion to improve crop yield in potato. Therefore, in this section, our aim was to estimate the expected direct selection response (*R*) for tuber yield and also for physiological traits, correlated selection response (*CR*), and efficiency of indirect selection (*CR*/*R*) for tuber yield from physiological traits. Mean values of F1 population were used to estimate the genetic correlations between physiological traits and measured tuber yield (Chapters 2 and 3); estimates for *R*, *CR*, and *CR*/*R* were estimated following the methods described by Falconer (1996) as:

$$R = iH_x^2\sigma_x \quad (6.1)$$

$$CR = iH_xH_yr_G\sigma_y \quad (6.2)$$

$$CR/R = H_yr_G/H_x \quad (6.3)$$

where, *i* is the selection differential (*i* = 1.76 at 10% selection intensity); $H_x^2$ and $\sigma_x$ are the heritability and phenotypic standard deviation values for trait x, respectively; $H_x$ and $H_y$ are the square root of the heritability of the trait x and y, respectively; $r_G$ is the genetic correlation between trait x and y, $\sigma_y$ is the phenotypic standard deviation for trait y.

The heritability and genetic correlations were estimated as per eqns 3.7 and 3.8, respectively (cf. Chapter 3). Values of *R*, *CR*, and *CR*/*R* were expressed as percentage of the genotypes mean for each trait in order to allow comparison among traits with different units (Table 6.3).

The results indicated high (>50%) expected or direct response to selection for physiological model traits: $D_{P2}$, $A_2$, $A_{sum}$, $c_m$, $t_E$, and *ED*. However, it was notable that direct selection response to tuber yield *per se* ($w_{max}$) was very low (i.e. only 29%) (Table 6.3). This was also supported by relatively lower proportion of genetic component of variance in the total phenotypic variance observed for tuber yield *per se* (Chapter 3). These results showed the added value and superiority of physiological traits over tuber yield *per se*.

The results furthermore indicated that correlated response to $w_{max}$ based on most physiological traits was higher than the direct selection for $w_{max}$. Using an alternative indirect selection tool for yield is appropriate if the genetic correlation between the target trait (e.g. yield) and component traits is very high, and the correlated response in the unselected trait based on the selected trait is higher than

**Table 6.3.** Genetic correlation coefficients ($r_G$) between physiological traits and measured tuber yield ($w_{max}$), expected selection response ($R$) for physiological traits and for $w_{max}$, correlated selection response ($CR$) and efficiency of indirect selection ($CR/R$) for $w_{max}$ estimated from physiological traits of potato. Estimations were based on F1 population mean across experiments. *td* stands for thermal day. For description about parameters, see Table 6.1.

| Trait | Unit | $r_G$ | $R$ | $CR$ | $CR/R$ |
|---|---|---|---|---|---|
| $t_{m1}$ | *td* | 0.24** | 0.31 | 0.06 | 0.29 |
| $t_1/D_{P1}$ | *td* | -0.05$^{NS}$ | 0.20 | -0.01 | -0.09 |
| $t_2$ | *td* | 0.70** | 0.22 | 0.22 | 0.57 |
| $t_e$ | *td* | 0.75** | 0.27 | 0.25 | 0.57 |
| $v_{max}$ | % | 0.84** | 0.18 | 0.23 | 0.94 |
| $c_{m1}$ | % *td*$^{-1}$ | 0.53** | 0.48 | 0.15 | 0.57 |
| $c_1$ | % *td*$^{-1}$ | 0.46** | 0.48 | 0.14 | 0.42 |
| $c_3$ | % *td*$^{-1}$ | 0.17** | 0.27 | 0.03 | 0.40 |
| $D_{P2}$ | *td* | 0.85** | 0.98 | 0.27 | 0.73 |
| $D_{P3}$ | *td* | 0.15** | 0.39 | 0.04 | 0.20 |
| $A_1$† | *td* % | – | – | – | – |
| $A_2$ | *td* % | 0.84** | 1.07 | 0.27 | 0.69 |
| $A_3$ | *td* % | 0.41** | 0.44 | 0.11 | 0.46 |
| $A_{sum}$ | *td* % | 0.78** | 0.49 | 0.26 | 0.59 |
| $c_m$ | g *td*$^{-1}$ | -0.20** | 0.78 | -0.06 | -0.16 |
| $t_E$ | *td* | 0.66** | 0.53 | 0.22 | 0.49 |
| *ED* | *td* | 0.64** | 0.93 | 0.21 | 0.48 |
| RUE | g DM MJ$^{-1}$ | -0.25** | 0.41 | -0.08 | -0.22 |
| N uptake | g m$^{-2}$ | 0.85** | 0.29 | 0.24 | 0.91 |
| NUE | g DM g$^{-1}$ N | 0.43** | 0.28 | 0.13 | 0.39 |
| $w_{max}$ | g m$^{-2}$ | | 0.29 | | |

** Significant at 1%, $^{NS}$ Non-significant.

† Estimation was not possible due to zero genetic variance ($\sigma^2_G$), see Table 2.3, Chapter 2.

the direct response to selection of the unselected trait (Falconer, 1996). Our results further indicated significant ($P$<0.01) and strong genetic correlations between tuber

yield and most of physiological model traits (Table 6.3). For instance, traits such as $t_2$, $t_e$, $v_{max}$, $c_{m1}$, $D_{P2}$, $A_2$, $A_{sum}$, $t_E$, $ED$, N uptake, and use efficiency showed very high (> 0.80) genetic correlations with $w_{max}$. The results therefore suggested that high indirect response could be obtained by selecting genotypes for these traits to improve tuber yield in potato. However, our results also suggested that while using these traits as a criterion for selection, their causal physiological inter-relationships and trade-offs must be considered simultaneously (see Fig. 3.6, Chapter 3). Finally, the results concluded that indirect selection efficiency of most physiological traits was higher than the direct selection efficiency for tuber yield. The selection efficiency from our physiological traits ranged up to 94% (Table 6.3). However, it was noted that efficiency of indirect selection was not high for traits like $c_m$ and RUE despite their high direct physiological relationship with tuber yield determination (Fig. 3.6, Chapter 3). This was mainly due to the weak phenotypic (Table 3.6, Chapter 3) as well as genetic correlations (Table 6.3) with tuber yield observed for these traits, mainly influenced by the strong negative indirect effects of $A_{sum}$ (as explained in the previous section).

According to our results, the relative importance of traits based on their (>50%) indirect selection efficiency for tuber yield determination can be ranked as: $v_{max}$ > N uptake > $D_{P2}$ > $A_2$ > $A_{sum}$ > $t_2$ > $t_e$ > $c_{m1}$. These findings strongly concluded that most physiological traits can be used successfully as indices of selection for yield improvement in potato.

This thesis thus indicated the direction and magnitude of correlated responses to selection for tuber yield and the relative efficiency of indirect selection. In addition, our results suggest that the development of such a selection index must integrate several key physiological traits, their inter-relationships and repeatability (high heritability) for assessing yield in breeding programmes (Baker, 1986; Bouman, 1995).

***QTL mapping of physiological traits***

While environmental characterisation and physiological knowledge help to explain and unravel gene and environment context dependencies, the analysis of gene effects on yield in diverse environments unmasks some of the key effects of genetic and environmental variability on the target trait. The phenotype of most plant characteristics varies quantitatively as it is under the influence both of the environment and of genetic factors encoded at quantitative trait loci (QTLs) (Gelderman, 1975). Understanding the basis of the interaction responses at the whole plant level (Reynolds et al., 2005; Raven et al., 2005; Trethowan et al., 2005) and

identifying QTL and molecular markers associated with desirable traits (Price et al., 2002; Nigam et al., 2005; Habash et al., 2007) are likely to have a large impact on the research aimed at improving yield in potato.

Many studies have identified QTLs for different traits in potato under normal conditions for various agronomic, and quality traits (e.g. Van den Berg et al., 1996; Van Eck et al., 1994; Schäfer-Pregl et al., 1998; Bradshaw et al., 2008). However, knowledge about genetic basis of important physiological traits closely linked to the temporal dynamics of yield formation and resource (radiation and N) use efficiencies is still limited and hardly any QTLs have been identified for these traits in potato. In other words, physiological aspects of complex quantitative traits in potato have so far received little attention from geneticists in QTL analysis although there are some recent studies that use statistical models to analyse data based on semi-quantitative scales describing canopy development (e.g. Hurtado et al., 2012).

In this study, our molecular dissection of traits determining the dynamics of canopy cover, tuber bulking, and resource (radiation, N) use efficiencies identified several QTLs, the mapping position of each identified QTL, the interaction of QTL with environment, and the magnitude of QTL effect on explaining genetic variance in both SH and RH parental genomes (Chapters 2 and 3).

The QTL results clearly showed that one particular chromosomal position at 18.2 cM on paternal (RH) linkage group V was controlling nearly all the traits (Tables 2.9 and 3.10), rendering the population on which this research was done less suitable, albeit it is agronomically well adapted. For example, it was notable that QTL for traits like $t_e$, $t_2$, $D_{P2}$, $A_2$, $A_{sum}$, $c_m$, $t_E$, $ED$, and tuber yield *per se* were co-localised in majority of the environments. This QTL was associated with major additive effects on most of the traits and explained more than 50% of the phenotypic variance. Strong genetic correlations among most of these traits (Chapters 2 and 3) and with tuber yield (Table 6.3) further supported these results and suggested pleiotropic nature of the QTL for most of the traits.

It is well known that linkage group V harbours the QTL for plant maturity and vigour in potato (Collins et al., 1999; Oberhagemann et al., 1999; Visker et al., 2003; Bradshaw, et al., 2008). Our results also confirmed this fact as most of the traits linked to this chromosome were related with maturity, for instance $D_{P2}$, $c_m$, $ED$, and $A_{sum}$ (Chapter 3). In other words, this thesis gave a clear picture about maturity in a SH × RH segregating population of potato and indicated that maturity is mainly expressed from the paternal (RH) side on linkage group V. It was further notable that this linkage group is mainly controlling earliness in genotypes on account of the negative additive effects associated with a major QTL found here for most of traits including tuber yield *per se* (Chapters 2 and 3). This information could be very useful

in elucidating the genetic basis of yield determination in early and late maturing genotypes.

The QTL-by-environment (QTL×E) interaction phenomenon was evident mainly for traits determining the canopy build-up and senescence phases, maximum canopy cover ($v_{max}$) rates of canopy growth and senescence ($c_{m1}$, $c_1$, and $c_3$), duration ($D_{P1}$) and area under canopy cover ($A_1$) when canopy cover reaches its maximum, duration ($D_{P3}$) and area under canopy cover ($A_3$) of canopy senescence, resource (radiation and N) use efficiencies and tuber yield *per se*. These results were expected due to the presence of relatively lower genetic variance than their G×E or E component of total phenotypic variance in these traits, as described in previous sections (see Tables 2.3 (Chapter 2) and 3.4 (Chapter 3)). Figure 6.5 illustrates such genetic complexity in tuber yield *per se*. Such inconsistencies in QTL behaviour can cause major problems in the detection of QTLs and their effective use in molecular breeding. However, such QTLs could be useful for marker assisted breeding for specific environments. Our thesis as a whole provided a better understanding of the genetic background of important physiological components traits determining maturity type as well as tuber yield in potato.

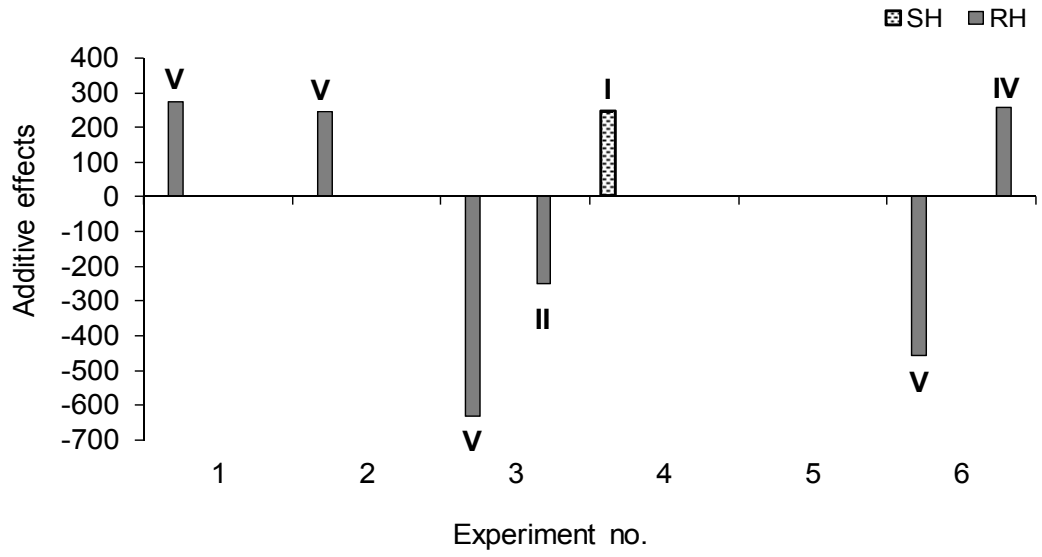


**Figure 6.5.** QTL×E additive effects for tuber yield (g $m^{-2}$) parental (SH and RH) genomes for six experiments. Letters above or below the bars indicate different linkage groups.

***An ecophysiological model to analyse genetic variation in tuber yield***

As already highlighted in previous sections, yield variation in terms of growth and development of the crop is complex, for it involves the effect of external factors on all the physiological processes, the inter-relationships between different processes and their dependence on the genetic constituent of the plant. One of the applications of processed-based ecophysiological crop growth models is their capability to explain differences in the yield potential of cultivars on the basis of individual physiological parameters, and the use of this knowledge for evaluating and designing plant types (Kropff et al., 1995; Yin et al., 2003c). This is possible because, as they become more mechanistic and comprehensive, crop-growth models can be used to mimic the genetic characteristics of plants (Chapter 1).

However, a major limitation of current crop models in accounting for G×E interactions is the low resolution and accuracy of the model in comparison to the subtle differences between genotypes commonly observed in many well-conducted multi-environment trials (White and Hoogenboom, 1996). A contrasting point of view is that crop physiological frameworks that are more readily aligned with plant breeders' modes of action are required (e.g. Shorter et al., 1991; Yin et al., 2004; Yin and Struik, 2008). Studies where simulation analyses of variation in a trait have been confirmed in the field are rare. Certainly, it seems logical that if crop models are to be incorporated into a crop improvement programme, it is essential that the parameters are easily and simply obtained so that breeders can use them and apply them without substantial investment in time and data collection.

Yin and Van Laar (2005), along the aforementioned lines of thinking, presented a crop model, GECROS (Genotype-by-Environment interaction on CROp growth Simulator), to overcome some of the weaknesses of earlier crop models. GECROS captures traits of genotype-specific responses to environment based on quantitative descriptions of complex traits related to the phenology, root system development, photosynthesis, stomatal conductance, and stay-green traits. GECROS uses new algorithms to summarise current knowledge of individual physiological processes and their interactions and feedback mechanisms (Chapter 5). It attempts to model each sub-process at a consistent level of detail, so that no process is overemphasised or requires too many parameters and similarly no process is treated in a trivial manner, unless unavoidable because of lack of understanding. GECROS also tries to maintain a balance between robust model structure, high computational efficiency, and accurate model output. The model can be used for examining responses of biomass and dry matter production in arable crops to both environmental and genotypic characteristics.

In this study (Chapter 5), we therefore examined the potential of the GECROS

crop growth model in predicting yield differences of individual genotypes in a segregating population of potato, their parents and a set of cultivars covering a wide range of maturity types. We focused mainly on the genotype-specific input parameters of the model. Table 5.1 (Chapter 5) gives the description of genotype-specific parameters of GECROS, which include $m_V$ and $m_R$ (i.e. period from plant emergence to onset of tuber bulking and duration between onset of tuber bulking and crop maturity, respectively); $H_{max}$, plant height; $N_{max}$, total crop N uptake at maturity; $n_{SO}$, maximum potato seed tuber N concentration. Calibration data for the model input parameters were obtained from our extensive data sets of Chapter 2 and 3. Procedures for estimation and correction for experiment-specific parameter values are described in Chapter 5.

The model described well the dynamics of important growth related processes in potato and gave important insights into the underlying component traits and factors influencing the tuber dry matter production. Using as few as five measured genotype-specific parameters (Table 5.1, Chapter 5), the model showed a good potential in explaining the observed yield differences among genotypes. Simulated trends of growth were in close agreement with the measured data (Fig. 5.3, Chapter 5). The model yielded reasonable predictions of differences in tuber yield across environments and across genotypes (Figs. 5.4 and 5.5).

Simulation models can be very useful to evaluate critical traits needed for high yield potential (Penning de Vries, 1991; Kooman and Haverkort, 1995; Yin et al., 2000b). The model based sensitivity analysis indicated that $N_{max}$ and $n_{SO}$ were the most important parameters of GECROS model as they contributed most to the determination of tuber yield (see Chapter 5, section 3.4) . The results suggested that genotypes with higher $N_{max}$ may exhibit more final tuber yield (Fig. 6.6), provided $n_{SO}$ is low or in other words genotypes with high NUE (Casa et al., 2005; Chapter 3). Our path coefficient analysis also further indicated that relationships of most physiological traits with tuber yield are actually driven mainly through plant's capability to uptake maximum N (Table 5.4, Chapter 5). These results further proved our earlier described results that plant N uptake could be proposed as a criterion to indirectly select for tuber yield.

This thesis therefore confirmed the usefulness of an ecophysiological model 'GECROS' in exploring the impact of new genotypes and the contribution of individual physiological traits on yield by simulating the responses of genotypes across different environments. In addition, our model analysis allowed us to identify the genotypic key parameters and shed light on some of the vital physiological mechanisms responsible for genotypic differences in tuber yield. The concepts captured in the model draw more attention to N uptake and use

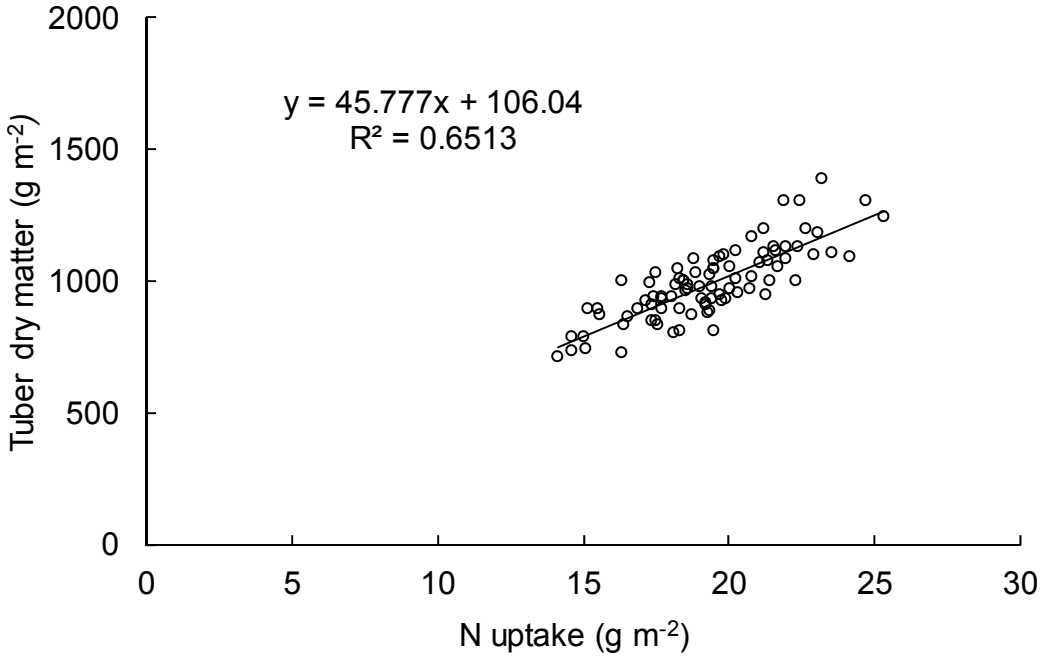


**Figure 6.6.** Relationships between measured plant N uptake and tuber dry matter in F1 population of potato across environments.

efficiency, as possible areas for improvements in tuber dry matter production.

The identification of both genotype-specific key parameters and main physiological processes involved in tuber yield formation should be useful from a genetic point of view. They could guide research towards these key processes and orientate breeding programmes as suggested by Yin et al. (2004). Further analysis of the genotypic parameters should be performed in conjunction with molecular markers in order to determine their genetic control. Such information would greatly facilitate the development of ideotypes for specific environments.

## Conclusions

The work presented in this thesis intends to increase our physiological knowledge of those factors applicable to plant breeding determining the yield of potato. We presented a robust physiological framework for quantitatively dissecting the phenotypic variation in potato growth and development to aid understanding of underlying causes while simultaneously providing means to predict emergent phenotypic consequences by integrating effects of variation in component factors and processes leading to yield formation in potato.

This thesis indicated that yield potential in potato can be enhanced by selecting for morphological, physiological, and phenological traits. Once this is accepted, the challenge is in finding which traits to modify and the optimum phenotype or expression for these traits. It was concluded that parameters of the growth functions determining the temporal dynamics of canopy cover and tuber bulking have a clear meaning with regards to the processes of resource capture by the plant, thus allowing a more easy interpretation of the value and magnitude of the growth components associated with variation in tuber yield among cultivars and/or genotypes. However, these components are not physiologically independent as genotypes with a high tuber bulking rate may effectively limit the crop growth and duration (via enhanced internal plant competition) leading to their identified 'earliness'.

In this context, this study also highlighted such trade-offs among key physiological traits causing subtle complexities in defining the maturity type in potato. Our results indicated that re-defining the maturity type of a large set of new genotypes based on physiological traits is possible and would prove useful. The new physiology-based maturity definition could allow relating the maturity to crop phenology and physiology and could help in designing potato ideotypes with specific maturity type for specific growing conditions and/or environments.

This study also highlighted the characterisation of the role of environments mainly N. Overall, results concluded that N availability is the driving factor for causing trade-offs between the physiological traits and different environments. Moreover, results suggested that N availability and its interaction with genotype's maturity type mainly contribute to the G×E interaction of the growth and development related processes in potato in a large set of F1 segregating (SH × RH) potato genotypes. This thesis therefore allowed a partial understanding of the environmental causes of the observed G×E interactions.

Our quantitative approach in combination with markers of the widely available and easy to use AFLP marker system identified QTLs that could be useful in the development of marker assisted breeding strategies in potato yield improvement. The QTL results showed that nearly all the physiological traits co-localised at one particular chromosomal position at 18.2 cM on paternal (RH) linkage group V with major effects. This QTL was associated with major additive effects on most of the traits and explained more than 50% of the phenotypic variance. This suggested the pleiotropic nature of the QTL for most of the traits determining crop maturity and tuber yields. A number of QTLs for traits were not detected when tuber yield *per se* was subjected to QTL analysis. The phenotypic variance explained by the QTLs for tuber yield *per se* was also lower than for other traits.

Our results also confirmed previous studies that most of the traits linked to

linkage group V were related with maturity. It was further notable that this linkage group is mainly controlling earliness in genotypes on account of the negative additive effects associated with a major QTL found here for most of traits including tuber yield *per se*.

The capability of an ecophysiological model 'GECROS' was tested in this thesis to analyse differences in tuber yield of potato and analyse the importance of genotype-specific model-input parameter towards tuber yield production. The model yielded a reasonably good prediction of differences in tuber yield across environments and across genotypes. Trends of growth and nitrogen uptake were adequately reproduced by the model. The GECROS model based sensitivity analysis indicated that total crop N uptake and tuber N concentration were the most important parameters of GECROS model as they contributed most to the determination of tuber yield. The results concluded that GECROS model is a useful tool in analysing the contribution of individual physiological traits to tuber yield by simulating the responses of genotypes across different environments. Further analysis of the genotypic parameters should be performed in conjunction with molecular markers. They could guide research towards key processes and orientate breeding programmes as suggested by Yin et al. (2004).

To conclude, breeding efforts aimed at meeting ongoing challenges, such as breaking yield barriers and improving performance under diverse environments, are more likely to achieve success if physiological understanding is used to compliment traditional breeding approaches. This thesis yielded estimates for agronomically relevant crop physiological and genetic characteristics and/or traits that are promising for defining future breeding strategies in potato. High genetic variability along with high heritability for most of these traits indicated that a more general breeding goal, increased tuber dry matter yield by indirectly selection for optimal combination of important physiological traits can be achieved. Results also indicated that while using these traits as a criterion for selection, the causal physiological relationships and trade-offs must be considered simultaneously.

The approach described in this thesis is promising for defining future breeding strategies in potato and the information obtained may help in designing ideotypes for specific and/or diverse environments as well as in marker assisted selection (MAS). As mentioned in Chapter 1, current approaches to MAS for complex traits lack good predictive power due to complex interactions among genes and/or environments. One strategy to overcome these difficulties would be to combine QTL and ecophysiological models, i.e. a step forward towards QTL-based crop modelling. However, small data sets for QTL mapping (i.e. only 88 genotypes, cf. Materials and Methods, Chapter 2) and lower numbers of independent QTLs found for single traits

(see Tables 2.8 (Chapter 2) and 3.9 (Chapter 3)) did not allow achieving this novel goal. In this context, future research should focus on this area and further steps should be taken in linking crop modelling with QTL mapping for physiological and genotypic traits generated by this thesis. We hope that the strong foundation set by this thesis would help in achieving broader goal of proceeding towards *model based* plant breeding (Chapter 1). On these lines, a follow up PhD research is currently well underway including the same SH × RH population as well as a very large set of cultivars are grown in experiments in which nitrogen supply is included as an experimental factor .

However, making significant contributions in these areas requires much closer collaborative research efforts between physiologists and plant breeders. Until such research is conducted, and the benefits of shifting resources into the systems approach can be weighed against reducing the resources put into the conventional empirical approach, widespread acceptance of the new methods is unlikely.

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# Summary

The sustained increase in global food production is unprecedented. A major challenge for plant and crop science is discovering new ways to continue to increase crop yield in a sustainable manner. Potato (*Solanum tuberosum* L.) is among the world's most important crops with a well-recognised role in human nutrition, food security, and national economy of many countries. Due to increasing food demand and changing diets potato is becoming a subsistence crop in many regions. However, the agronomy and whole crop physiology of tuber yield production are difficult as each developmental stage in potato is likely to be regulated and controlled by a large set of interacting expressed genes and because the genotype-by-environment (G×E) interactions are strong. Breeding for highly-yielding crop cultivars for specific environments and the prediction of their behaviour are major challenges. New technologies must be developed to accelerate breeding through improving genotyping and phenotyping methods and by increasing the available genetic diversity in breeding germplasm.

Interventions in breeding based on understanding of the genetic and physiological basis of crop performance have the potential to accelerate genetic gains for yield and resource use efficiency. The genetic improvement of yield can be understood more mechanistically by investigating and interpreting the relationships between the main attributes of growth. Such studies may shed light on potential future alternatives for sustainable yield improvement.

Crop modelling can play a significant part in system approaches by providing a powerful tool for phenotype prediction and yield scenario analysis; to explore the impact of new genotypes and the contribution of individual physiological traits on yield by simulating genotypes under various environmental scenarios and management options. Modelling may also prove useful in understanding G×E, thus helping to speed up the currently stagnant pace of crop improvement. Nevertheless, insights into the physiological processes leading to yield development and the factors affecting these processes are still underdeveloped.

This thesis aims to develop an approach to quantify and predict the yield of individual genotypes and to estimate parameters which may reveal the effects of genetic and environmental factors on important plant processes controlling tuber yield variation. The analysis conducted in this thesis is based primarily on data collected from six contrasting field experiments carried out in Wageningen (52° N latitude), the Netherlands, during 2002, 2004 and 2005. The plant material used in this study consisted of 100 F1 diploid (2n = 2x = 24) potato genotypes derived from a

cross between two diploid heterozygous potato clones, SH83-92-488 × RH89-039-16. Five standard cultivars (Première, Bintje, Seresta, Astarte, and Karnico) and the parental clones were also included in this study.

The thesis is composed of six chapters. **Chapter 1** gives an overview of complications in dealing with quantitative traits like yield and highlights the role of systems approaches via incorporating crop modelling and crop physiological knowledge in potato breeding programmes. It presents the possible opportunities from such combined efforts towards reinforcing the genetic analysis of complex traits.

**Chapter 2** presents a quantitative model approach based on the beta function to analyse the time course of canopy cover during the entire crop cycle as a function of thermal time. The model describes the canopy development dynamics in three phases (build-up phase, maximum cover phase, canopy decline phase) through five parameters defining the timing and duration of the phases and maximum canopy cover ($v_{max}$). These five parameters were further used to derive secondary traits, related to rate of increase or decrease of canopy cover, and the area under whole green canopy cover curve ($A_{sum}$). The latter trait $A_{sum}$ was directly related to the ability of the genotypes to intercept photosynthetically active radiation (PAR) and thus to realize tuber yield. The model successfully described quantitative differences in canopy dynamics of a diverse set of genotypes in a segregating F1 population of potato under varied environments.

The results indicated that length of the canopy build-up phase ($t_1$ or $D_{P1}$) was conservative, but the duration of maximum canopy cover ($D_{P2}$) and the decline phase ($D_{P3}$) varied greatly, with later genotypes having similar $D_{P1}$, but longer $D_{P2}$ and $D_{P3}$ and thus generate higher values of $A_{sum}$. Strong positive phenotypic and genetic correlations were observed between $D_{P2}$ and $v_{max}$, indicating that genotypes with longer $D_{P2}$ could be indirectly obtained by selecting genotypes with maximum value of canopy cover ($v_{max}$). For most traits quantified in the model, high genetic variability and high heritability were recorded. Genetic variance contributed greatly to the total phenotypic variance for most traits, for instance, time of onset ($t_2$) or end of canopy senescence ($t_e$), $D_{P2}$, and $A_{sum}$, indicating their strong genetic background and stability across environments.

Several QTLs were detected across the experiments for the model parameters and derived traits determining the canopy dynamics. One particular chromosomal position at 18.2 cM on paternal (RH) linkage group V was controlling nearly all the traits and showed its pleiotropic nature. This QTL had major additive effects and explained 74% of the phenotypic variance. Most of the traits linked to this linkage group were related with earliness. Such information could be very useful in identifying the genetic basis of maturity type in potato. This chapter yielded estimates

for agronomically relevant crop characteristics that could be promising for defining future breeding strategies for traits influencing the radiation interception and thereby final yield.

**Chapter 3** describes a quantitative model approach to analyse the dynamics of tuber bulking during the entire crop cycle as a function of thermal time using a piece-wise expolinear function. The model breaks down tuber growth into parameters related with the growth rate and effective duration of the linear phase of tuber bulking. Furthermore, radiation- and nitrogen use efficiencies (RUE and NUE, respectively), and their relationships with the model parameters are also studied. Rate of tuber bulking ($c_m$) was highest for early-maturing genotypes followed by mid-late and then late genotypes. On the other hand, late-maturing genotypes had longest effective duration of tuber bulking (*ED*) followed by mid-late and early genotypes. As a result, final tuber yield ($w_{max}$) was higher in late genotypes than in early genotypes. The results further illustrated that RUE values were highest for early-maturing genotypes followed by mid-late and late genotypes whereas NUE was highest in late-maturing genotypes followed by mid-early and early genotypes. The phenotypic and genetic correlations suggested physiological trade-offs between $c_m$ and *ED* as well as between RUE and NUE. High genetic variability along with high heritability was recorded for most traits which illustrated their strong genetic background. Path coefficient analysis showed that RUE, $c_m$, and $A_{sum}$ (previously defined in Chapter 2), had a major influence on $w_{max}$. Sixteen QTLs were detected for traits studied in this chapter, explaining the phenotypic variance by up to 79%. In accordance with Chapter 2, QTLs controlling most of the traits were detected at position 18.2 cM on paternal (RH) linkage group V with major additive effects and explained most of the total phenotypic variance. Our results indicated that a number of QTLs for traits were not detected when tuber yield *per se* was subjected to QTL analysis. The phenotypic variance explained by the QTLs for tuber yield *per se* was also lower than for other traits. This suggests that complex traits like these are controlled by QTLs that often show low stability across environments. Overall, parameters found in this chapter indicated that there are opportunities for improving tuber dry matter yield in potato by selection for optimal combination of important physiological traits like RUE, $c_m$, and $A_{sum}$.

**Chapter 4** addresses the issue of maturity type in potato, as currently there are so many unclear interpretations. This chapter tries to create a clear and consistent definition of the concept of maturity type and presents an approach to assess the maturity type in a large set of potato genotypes in a rather simple and reproducible way. The added physiological and quantitative knowledge gained from Chapters 2 and 3 were used to quantify maturity type unambiguously for a set of varieties and a

segregating population across diverse environments. The re-defined physiological based maturity criteria are based on four traits: $D_{P2}$, $c_m$, $ED$, and $A_{sum}$. The re-defined, four physiological maturity criteria were compared with the conventionally used criterion. The results indicated that physiological maturity type criteria tended to define maturity classes less ambiguously in comparison to the conventional criterion. Moreover, the conventional criterion was subject to more random noise and lacked stability and/or repeatability with respect to physiological quantitative traits. The re-defined criteria also clearly illustrated the physiological trade-offs that existed between the selected traits and underlined the subtle complexities in defining the maturity type. The new definition would not only allow relating maturity to crop phenology and physiology but could also offer wider applications in potato breeding and crop management studies. One such application would be to help in designing strategies for potato ideotype breeding for genotypes with specific maturity types.

**Chapter 5** sheds light on some of the key mechanisms causing genotype differences in tuber yield and provides support for important aspects of hypothesis regarding nitrogen accumulation. It tests the capability of the generic ecophysiological model 'GECROS' to analyse differences in tuber yield of potato within an F1 population, the parents, and a set of cultivars. The model predicts crop growth and development as affected by genetic characteristics and climatic and edaphic environmental variables. The genotype-specific model-input parameter values were estimated and the model was used for predicting the tuber yield of afore-mentioned plant material in multiple field experiments. The model was reasonably good in predicting the differences in tuber yield across environments and across genotypes. Trends of growth and nitrogen uptake were adequately reproduced by the model. Model analysis identified the genotypic key-parameters affecting tuber yield production and $N_{max}$ (i.e. total crop N uptake) contributed most to the determination of tuber yield. The results showed that genotypes with higher $N_{max}$ and lower tuber N content exhibited higher tuber dry matter yield. Such information can greatly facilitate the development of potato ideotypes for specific environments. The results confirmed that the GECROS model is useful for exploring the impact of new genotypes and the contribution of individual physiological traits on yield by simulating the responses of genotypes across different environments.

**Chapter 6** finally discusses the main findings and overall contribution of this thesis. It indicates ways to enhance the power of molecular breeding strategies as well as ideotype breeding in potato. It stresses upon the use of combined knowledge from the fields of crop physiology, modelling, and genetics in elucidating and understanding the complex traits. Such an integrated approach can reinforce the genetic analysis of complex traits like yield, thereby improving breeding efficiency. In

this context, future research should focus on this area and further steps should be taken in linking crop modelling with QTL mapping for physiological and genotypic traits generated by this thesis. The strong base set by this thesis could help in achieving this broader goal of *model based* plant breeding. However, to make such significant strides, much closer collaborative research efforts between physiologists and plant breeders are direly needed

# Samenvatting

Wereldwijd blijft de vraag naar voedsel toenemen. Een grote uitdaging voor plant- en gewaswetenschappen is het ontdekken van nieuwe manieren om op een duurzame manier de gewasopbrengsten te blijven verhogen. De aardappel (*Solanum tuberosum* L.) is één van de belangrijkste gewassen in de wereld. Het gewas speelt een belangrijke rol in de humane voeding, voedselzekerheid, en de nationale economie van vele landen. Door de toenemende vraag naar voedsel en veranderende voedingspatronen wordt de aardappel in vele regio's een belang-rijker basisvoedsel. In het algemeen zijn agronomie en gewasfysiologie van opbrengstvorming lastig aangezien elk ontwikkelingsstadium waarschijnlijk wordt gereguleerd en gecontroleerd door een grote reeks tot expressie gebrachte en op elkaar inwerkende genen en omdat de genotype×milieu (G×E) interacties sterk zijn. Veredeling voor hoog-opbrengende rassen voor specifieke milieus en het voorspellen van hun gedrag zijn daarbij belangrijke uitdagingen. Nieuwe technologieën moeten worden ontwikkeld om het veredelingsproces te versnellen. Denk aan verbeterde methoden voor genotypering en fenotypering, alsmede modellen die het fenotype voorspellen uit het genotype. Daarmee kan bestaande en nieuwe genetische diversiteit beter benut worden in het veredelingsproces.

Inzicht in de genetische en fysiologische basis van opbrengstvorming kan bijdragen aan meer efficiënte selectiemethoden voor de gewenste genetische aanleg, in het bijzonder voor eigenschappen die bijdragen aan betere benutting van de hulpbronnen licht en stikstof (RUE, NUE). De genetische opbrengst-verbetering kan meer mechanistisch worden begrepen door het onderzoeken en interpreteren van de relaties tussen de belangrijkste groeikarakteristieken. Door het onderzoeken en interpreteren van de relaties tussen de belangrijkste processen tijdens de groei en ontwikkeling van de plant in genetisch divers materiaal kan meer specifiek gestuurd worden in de veredeling van opbrengst-componenten. Dergelijke studies kunnen licht werpen op mogelijke toekomstige alternatieven voor duurzame opbrengstverbetering.

Gewasmodellering kan een belangrijke rol spelen in systeembenaderingen omdat modellen krachtige instrumenten zijn voor het voorspellen van het fenotype en voor het analyseren van opbrengstscenarios. Modellen kunnen ook behulpzaam zijn bij verkennen van het opbrengstpotentieel van nieuwe genotypen en van de bijdrage van individuele fysiologische kenmerken aan deze opbrengst, omdat ze gebruikt kunnen worden voor het simuleren van de groei van genotypen onder verschillende milieu-scenario's en teelttechniek. Modellering kan ook nuttig zijn bij

het begrijpen van G×E. Toch zijn de inzichten in de fysiologische processen die leiden tot de opbrengstvorming en de factoren die van invloed zijn op deze processen nog onderontwikkeld.

Dit proefschrift beoogt een aanpak te ontwikkelen voor het kwantificeren en voorspellen van de opbrengst voor individuele genotypen en voor het schatten van relevante parameters. Het gaat daarbij om parameters die de effecten kunnen blootleggen van genetische factoren en omgevingsfactoren op belangrijke plantprocessen die gezamenlijk de variatie in knolopbrengst bepalen. De analyse in dit proefschrift is hoofdzakelijk gebaseerd op gegevens die zijn verzameld in zes contrasterende veldexperimenten uitgevoerd nabij Wageningen (52° Noorderbreedte), Nederland, in de jaren 2002, 2004 en 2005. Het plantmateriaal in deze studie bestond uit een diploïde F1 populatie (2n = 2x = 24) van 100 nakomelingen verkregen uit een kruising tussen twee heterozygote diploïde aardappelklonen, SH83-92-488 en RH89-039-16. Vijf standaardrassen (Première, Bintje, Seresta, Astarte en Karnico) en de oorspronkelijke ouderklonen werden ook opgenomen in deze studie.

Het proefschrift bestaat uit zes hoofdstukken. **Hoofdstuk 1** geeft een overzicht van complicaties in het omgaan met kwantitatieve kenmerken zoals opbrengst en benadrukt de rol van de systeembenaderingen via het inpassen van gewasmodellering en gewasfysiologische kennis in aardappelveredelings-programma's. Het presenteert de mogelijkheden van dergelijke gecombineerde inspanningen om te komen tot een genetische analyse van complexe eigenschappen.

In **Hoofdstuk 2** wordt een kwantitatieve modelbenadering op basis van de bètafunctie gepresenteerd om het verloop van de bodembedekkingsgraad te analyseren tijdens de gehele gewascyclus als functie van de thermotijd. Het model beschrijft de dynamiek van de ontwikkeling van de bodembedekkingsgraad in drie fasen (opbouwfase, fase van maximale bodembedekking, afstervingsfase). Het doet dat door middel van vijf parameters die samen aanvang, eind en duur van de drie fasen bepalen alsmede de maximale bedekkingsgraad ($v_{max}$). Deze vijf parameters werden verder gebruikt om secundaire kenmerken te schatten, gerelateerd aan snelheid van toe- of afname van de bedekkingsgraad, en de oppervlakte onder de totale curve van de bodembedekking tegen de thermotijd ($A_{sum}$). Deze laatste eigenschap, $A_{sum}$, was direct gerelateerd aan het vermogen van de genotypen om fotosynthetisch actieve straling (PAR) te onderscheppen en dus om knolopbrengst te realiseren. Het model beschreef met succes kwantitatieve verschillen in dynamiek in bodembedekking van deze genetisch diverse set van genotypen in een uitsplitsende F1 populatie van aardappel geteeld onder uiteenlopende omstandigheden.

De resultaten gaven aan dat de lengte van de opbouwfase van de bodem-

bedekking ($t_1$ of $D_{P1}$) conservatief was, maar de duur van de maximale bodembedekkingsgraad ($D_{P2}$) en de duur van de fase van afsterving ($D_{P3}$) liepen uiteen, waarbij latere genotypen vergelijkbare $D_{P1}$, maar langere $D_{P2}$ en $D_{P3}$ hadden en dus hogere waarden voor $A_{sum}$ genereerden. Er werden sterke, positieve fenotypische en genetische correlaties gevonden tussen $D_{P2}$ en $v_{max}$, hetgeen aangeeft dat genotypen met een langere $D_{P2}$ indirect zouden kunnen worden verkregen door het selecteren van genotypen met een hoge waarde voor de maximale bodembedekkingsgraad ($v_{max}$). Voor de meeste met het model gekwantificeerde eigenschappen was de F1 populatie uitermate variabel in vergelijking met de standaardrassen. Voor de meeste eigenschappen werd een hoge erfelijkheidsgraad waargenomen; met andere woorden de genetische variantie droeg in belangrijke mate bij aan de totale fenotypische variantie. Dit was bijvoorbeeld het geval voor tijdstip van aanvang ($t_2$) of het einde van loofafsterving ($t_e$), $D_{P2}$, en $A_{sum}$, duidend op een sterke genetische basis en stabiliteit over milieus.

Over de verschillende milieus werden voor de modelparameters en afgeleide kenmerken die de bodembedekkingsdynamiek bepalen verschillende QTLs gedetecteerd. De ouder RH89-039-16 bleek heterozygoot voor een bijzonder genetische locus op 18.2 cM op chromosoom 5. De uitsplitsende allelen van deze ouder bepaalden in de nakomelingen bijna alle gemeten eigenschappen en toonden zo een pleiotroop karakter. De andere ouder SH83-92-488 splitste voor deze locus niet uit. De allelen van deze locus (QTL) had grote additieve effecten en verklaarde tot 74% van de fenotypische variantie. Er was sprake van genetische koppeling tussen QTLs voor vroegheid en modelparameters. Dergelijke informatie kan zeer nuttig zijn bij het identificeren en karakteriseren van de genetische factoren betrokken bij vroegrijpheid in aardappel en daaraan gerelateerde kenmerken. Dit hoofdstuk leverde schattingen op voor landbouwkundig relevante gewaskenmerken die veelbelovend kunnen zijn voor het bepalen van toekomstige veredelingsstrategieën voor eigenschappen die de lichtonderschepping, en daarmee uiteindelijk de opbrengst, beïnvloeden.

**Hoofdstuk 3** beschrijft een kwantitatieve modelbenadering waarmee de dynamiek van de knolgroei gedurende de gehele gewascyclus werd geanalyseerd als functie van de thermotijd met behulp van een in trajecten opgedeelde expolineaire functie te analyseren. Het model ontleedt knolgroei tot parameters die betrekking hebben op de groeisnelheid en de feitelijke duur van de lineaire fase van knolvorming. Bovendien werden de gebruiksefficiëntie van straling en stikstof (respectievelijk RUE en NUE), en hun relaties met de modelparameters bestudeerd. Snelheid van knolvorming ($c_m$) was het hoogst voor de vroegrijpe genotypen gevolgd door middellate en dan late genotypen. Anderzijds, laatrijpe genotypen hadden de langste

knolvormingsduur (*ED*) gevolgd door middellate en vroege genotypen. Dientengevolge was de uiteindelijke knolopbrengst ($w_{max}$) hoger voor de late genotypen dan voor de vroege genotypen. Er werd tevens gevonden dat de waarden voor RUE het hoogst waren voor vroegrijpe genotypen, gevolgd door middellate en late genotypen, terwijl NUE juist het hoogst was in late genotypen, gevolgd door middelvroege en vroege genotypen. De waargenomen fenotypische en genetische correlaties suggereren dat er om fysiologische redenen een afruil bestaat tussen $c_m$ en *ED.* Hetzelfde geldt tussen RUE en NUE. Voor de meeste kenmerken werd een hoge genetische variatie en een hoge erfelijkheidsgraad gevonden, suggererend dat ze in sterke mate genetisch bepaald zijn. Padcoëfficiëntanalyse toonde aan dat RUE, $c_m$, en $A_{sum}$ (eerder beschreven in Hoofdstuk 2) een grote invloed op $w_{max}$ hadden. Voor de eigenschappen die in dit hoofdstuk werden bestudeerd werden 16 QTLs gedetecteerd, die maximaal 79% van de fenotypische variantie verklaarden. Overeenkomstig met wat in Hoofdstuk 2 werd gevonden, beheerste de locus op positie 18.2 cM van de vaderlijke (RH) koppelingsgroep V het grootste deel van de eigenschappen. Voor alle eigenschappen vertoonde deze locus grote additieve effecten en verklaarde het grootste deel van de totale fenotypische variantie. Onze resultaten laten zien dat een aantal QTLs die voor de deeleigenschappen werden gedetecteerd niet werden gevonden wanneer knoldrogestofopbrengst *per se* werd onderworpen aan een QTL analyse. De fenotypische variantie verklaard door de QTLs voor knoldrogestofopbrengst *per se* was ook lager dan voor andere eigenschappen. Dit suggereert dat complexe eigenschappen als knoldrogestofopbrengst worden gecontroleerd door QTLs die vaak slechts in beperkte mate stabiel zijn over de milieus. Over het geheel genomen gaven de parameters in dit hoofdstuk aan dat er kansen zijn om de knoldrogestofopbrengst in aardappel te verbeteren door selectie op een optimale combinatie van belangrijke fysiologische eigenschappen, zoals RUE, $c_m$, en $A_{sum}$.

**Hoofdstuk 4** gaat in op de kwestie van vroegheid in aardappel, omdat momenteel veel onduidelijk is over dit concept. Dit hoofdstuk probeert een eenduidige en consistente definitie van het begrip vroegheid te geven en geeft een benadering om vroegheid te bepalen in een grote reeks aardappelgenotypen, op een vrij eenvoudige en reproduceerbare manier. De nieuwe fysiologische en kwantitatieve kennis opgedaan in de Hoofdstukken 2 en 3 werd gebruikt om vroegheid eenduidig te kwantificeren voor een set van rassen en een uitsplitsende populatie geteeld in diverse milieus. De nieuwe definitie van vroegheid werd gebaseerd op vier verschillende fysiologische kenmerken: $D_{P2}$, $c_m$, *ED* en $A_{sum}$. De vier nieuwe, fysiologische vroegheidscriteria werden vergeleken met het gebruikelijke criterium. De resultaten gaven aan dat de fysiologische vroegheidscriteria doorgaans

de vroegheidsklassen op een minder dubbelzinnige manier definieerden dan het conventionele criterium. Bovendien gaf het conventionele criterium meer ruis en was het minder stabiel en minder herhaalbaar dan de fysiologische kenmerken. De nieuwe criteria blijken overigens ook de fysiologische wisselwerkingen te onderstrepen die bestonden tussen de geselecteerde eigenschappen en onderstreepten tevens de complexiteit van vroegheid bij aardappel. De nieuwe definitie maakt het niet alleen mogelijk vroegheid te relateren aan fenologie en fysiologie, maar kan ook breed worden toegepast in de aardappelveredeling en onderzoek naar de teeltechniek van aardappel. Eén van die toepassingen zou kunnen zijn het ontwerpen van strategieën voor veredeling van aardappelideotype voor specifieke vroegheids-klassen.

**Hoofdstuk 5** werpt licht op enkele van de belangrijkste mechanismen die er toe leiden dat genotypen verschillen in knoldrogestofopbrengst en biedt houvast voor belangrijke veronderstellingen aangaande de ophoping van stikstof. Het test de mogelijkheid om met het generieke gewasgroeimodel GECROS ecofysiologische verschillen in knoldrogestofopbrengst van nakomelingen uit een F1 populatie, de ouders, en een reeks cultivars te analyseren. Het model voorspelt de groei en ontwikkeling van gewassen onder invloed van genetische kenmerken en bodem- en klimaatfactoren. De genotype-specifieke model-input parameterwaarden werden geschat en het model werd gebruikt voor het voorspellen van de knolopbrengst van voornoemd plantmateriaal in verschillende veldexperimenten. Het model voorspelde de verschillen in knoldrogestofopbrengst over omgevingen en tussen genotypen tamelijk goed. Het model reproduceerde op adequate wijze de trends in groei en stikstofopname. Met behulp van de modelanalyse konden de belangrijkste genotypische parameters worden geïdentificeerd die van invloed zijn op de knoldrogestofopbrengst. De $N_{max}$ (de maximale totale N opname) droeg het meest bij aan de uiteindelijke knoldrogestofproductie. De resultaten toonden aan dat genotypen met een hogere $N_{max}$ en een lager N-gehalte in de knol een hogere knoldrogestofopbrengst hadden. Dergelijke informatie kan aanzienlijk bijdragen aan de ontwikkeling van aardappelideotypen voor specifieke omgevingen. De resultaten bevestigden dat het model GECROS handig is voor het verkennen van het belang van nieuwe genotypen en van de bijdrage van individuele fysiologische eigenschappen aan de opbrengst door het simuleren van de reacties van genotypen in verschillende milieus.

**Hoofdstuk 6** behandelt tot slot de belangrijkste bevindingen en de algemene bijdrage van dit proefschrift aan de wetenschap. Het geeft manieren aan om moleculaire veredelingsstrategieën en ideotypeveredeling in de aardappel te versterken. Het benadrukt de noodzaak om kennis op de terreinen van de

gewasfysiologie, modellering, en de genetica te combineren teneinde complexe eigenschappen beter te begrijpen. Een dergelijke geïntegreerde aanpak kan de genetische analyse van complexe eigenschappen zoals opbrengst versterken en verhoogt aldus de efficiëntie van het veredelen. In dit verband dient toekomstig onderzoek zich te richten op dit gebied en dienen verdere stappen te worden genomen om gewasmodelleren te koppelen aan QTL mapping van de fysiologische en genotypische eigenschappen die in dit proefschrift zijn beschreven. Dit proefschrift legt een stevige basis voor het bredere doel van door gewasmodellen ondersteunde plantenveredeling. Echter, dergelijke stappen kunnen alleen gezet worden als de samenwerking tussen fysiologen en genetici geïntensiveerd wordt.

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This thesis is a step towards understanding of genetic variation among a large set of potato genotypes. This study is a part of an extensive research effort to explore the possibilities to link crop physiology, modelling, and genetic analysis for a better understanding of potato growth and development that may help in understanding the yield dynamics as well as in designing ideotypes for specific and/or diverse environments. This thesis has resulted into four years and more of field and laboratory experimentation, literature review, data collection and modelling and genetic analysis. I sincerely hope that this thesis will, albeit modestly, contribute to the scientific knowledge of potato science.

Pursuing this PhD project with so many interesting facets was indeed a lovely and memorable experience for me. It was just like climbing a high peak, step by step, accompanied with challenges, hardships, encouragement, and hope. Now when I find myself at the top enjoying the beautiful scenery, I realise that it was in fact possible due to excellent team work that got me here finally.

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Muhammad Sohail Khan
Wageningen, September 2012

# Curriculum vitae

Muhammad Sohail Khan was born on 6th June 1981 in Khyber Pakhtunkhwa, Pakistan. He completed his basic education in 1998 and a few months later he entered as a student at the Faculty of Agriculture, Gomal University, Dera Ismail Khan, Khyber Pakhtunkhwa, Pakistan. In 2002, he obtained his 4-yr B.Sc. (Hons) Agriculture diploma with distinction. He continued his studies in the same university for his Masters and obtained his 2-yr M.Sc. (Hons) Agriculture diploma with distinction (Gold Medal) in 2004. He chose to specialize in the field of Horticulture during his Masters studies and worked on evaluating the effects of different auxins on the growth and establishment of Damask Rose (*Rosa damascena* Mill.) cuttings in different growing media.

Soon after completing his Masters, he briefly worked as a Research Assistant at the Arid Zone Research Institute Dera Ismail Khan, Pakistan Agricultural Research Council (PARC). His work mostly involved developing improved production and propagation technologies for arid horticultural fruits. In 2005, he was appointed as a Research Officer at the Horticulture Section of Agricultural Research Institute (ARI), Dera Ismail Khan under the auspices of Agricultural Research Government of Khyber Pakhtunkhwa, Pakistan. He was mainly involved in the conservation of elite indigenous fruit germplasm as well as multi-environment evaluation of different exotic cultivars of important regional fruits: Datepalm (*Phoenix dactylifera*), Mango (*Mangifera indica* L.), Ber (*Zizyphus jujuba* L.), Falsa (*Grewia asiatica*), etc. It is there that he became fascinated with studying the role of G×E interaction on plant growth and physiology.

In early 2007, he was awarded an "Overseas PhD Scholarship" from the Higher Education Commission of Pakistan (HEC) in collaboration with the Netherlands Organization for International Cooperation in Higher Education (NUFFIC). A few months later, he came to Wageningen University, the Netherlands to pursue his PhD study under the supervision of Prof. dr. ir. Paul C. Struik (Centre for Crop Systems Analysis, (CSA)), Prof. dr. ir. Fred A. van Eeuwijk (Biometris), Dr. Xinyou Yin (CSA), and Dr. ir. Herman J. van Eck (Laboratory of Plant Breeding). His PhD research was on "Assessing genetic variation in growth and development of potato (*Solanum tuberosum* L.)" which resulted into the outcome of this thesis. After defending his PhD thesis, he will join his parent institute in Pakistan. He has developed a strong interest in crop physiology, quantitative genetics, and *model-based* plant breeding. He would like to invest his future research efforts excelling in these areas.

# PE&RC PhD Education Certificate

With the educational activities listed below the PhD candidate has complied with the educational requirements set by the C.T. de Wit Graduate School for Production Ecology and Resource Conservation (PE&RC) which comprises of a minimum total of 32 ECTS (= 22 weeks of activities)

**Writing of project proposal (6 ECTS)**

- Genotype-by-environment (G×E) interaction on the dynamics of yield formation in potato (*Solanum tuberosum* L.) (2012)

**Writing of project proposal (4.5 ECTS)**

- Assessing genetic variation in growth and development of potato (*Solanum tuberosum* L.) (2008)

**Post-graduate courses (6 ECTS)**

- Art of modelling; PE&RC (2008)
- Modern statistics for the life sciences; Biometris (2009)
- Multivariate analysis; PE&RC (2010)

**Deficiency, refresh, brush-up courses (3 ECTS)**

- Crop ecology (2008)
- Systems analysis, simulation and systems management (2008)

**Competence strengthening / skills courses (6.6 ECTS)**

- Information literacy, including introduction to Endnote; WGS (2008)
- Project and time management; WGS (2008)
- Scientific writing; CENTA (2009)
- Techniques for writing and presenting scientific papers; WGS (2009)
- Presentation skills; CENTA (2010)
- How to write a world-class paper; Library Wageningen UR (2011)

**PE&RC Annual meetings, seminars and the PE&RC weekend (1.2 ECTS)**

- PE&RC Weekend (2008)
- PE&RC Day (2010)

**Discussion groups / local seminars / other scientific meetings (5.8 ECTS)**

- SENSE Context symposium; Wageningen UR, the Netherlands (2007)
- On the evolution of plant-pathogen interactions: from principles to practices; Wageningen UR, the Netherlands (2008)
- 40 Years theory and model at Wageningen UR, the Netherlands (2008)
- Plant roots from gene to ecosystem; Radboud University, the Netherlands (2008)
- Ecology and experimental plant sciences 2; Wageningen UR, the Netherlands (2009)
- Biometris statistical genetics meeting (2009-2012)
- The potato root system; Plant Breeding, Wageningen UR, the Netherlands (2010)
- Young PSG meetings (2010)
- Plant sciences seminars (2010-2012)
- Plant Breeding in the genomics era; Wageningen UR, the Netherlands (2011)

**International symposia, workshops and conferences (5.6 ECTS)**

- International Eucarpia Congress, "Potato breeding after completion of the DNA sequence of the potato genome"; Wageningen UR, the Netherlands (2010)
- International symposium on agronomy and physiology of potato, "Potato Agro-physiology-2010"; Nevşehir, Turkey (2010)

**Lecturing / supervision of practical's / tutorials (0.6 ECTS)**

- Research methods in crop science; 2 days (2010)

**Supervision of 4 MSc students; 7 days**

- Model based estimation of parameters describing the dynamics of canopy cover growth in a large set of potato (*Solanum tuberosum* L.) genotypes
- Estimation of beta thermal time
- Non-linear regression in SAS
- Mixed model analysis in Genstat

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