THE EFFECT OF TEMPERATURE ON PHENOLOGICAL RESPONSES AND GROWTH OF CANOLA CULTIVARS

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Thesis presented for partial fulfillment of the requirements for the degree Master of Science in Agriculture at the University of Stellenbosch

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December 2014

Declaration

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ABSTRACT

Canola is increasingly becoming an important economic field crop in South Africa, because it can be used to produce high quality cooking oil and margarine, animal feed, biofuel and in crop rotation systems to break the disease cycle and improve weed management. Effect of temperature on phenological responses with respect to required number of days, growing degree days, photothermal units to specific growth stages, growth rate, as well as vegetative and reproductive growth of canola were studied under controlled conditions.

Seven canola cultivars selected from early and mid-maturing groups of canola cultivars, presently planted in the Western Cape canola production area, were grown in 3 litre plastic bags filled with a mixture of sand and compost at ratio of 1:1 and irrigated with fully balanced nutrient solution at EC=2.0 in two glasshouses at night/day temperature regimes of 10/15^{o}C and 15/20^{o}C. Number of days, growing degree days (GDD) and photothermal units (PTU) from planting to seedling emergence, first true leaf appearance, visible flower buds, first flower opening, seed ripening and seed physiological maturity were recorded. Plant heights were measured at 14 day intervals from 28 to 84 days after planting (DAP). Plants were sampled for leaf area (LA) and above ground dry mass (DM) at budding, flowering and seed physiological maturity. Plant growth rates (PGR) from planting to budding, from budding to flowering and from flowering to physiological maturity were calculated. Relative growth rates (RGR) and net assimilation rates (NAR) from budding to flowering and from flowering to physiological maturity were also calculated. Days after planting, GDD and PTU at budding, flowering and physiological maturity were correlated with leaf area, dry mass, number of pods plant^{-1} and pod dry mass plant^{-1} at budding, flowering and physiological maturity to determine whether there were relationships between the variables.

The study showed that by increasing night/day temperature from 10/15ºC to 15/20ºC plant height, number of leaves plant^{-1} at budding stage, leaf area at budding , plant growth rate (PGR) from planting to budding stage and relative growth rate (RGR) from budding to flowering stage were increased. However, PGR from budding to physiological maturity, RGR from flowering to physiological maturity, net assimilation rate (NAR) from budding to flowering stage, leaf area at flowering and physiological

maturity stages , as well as number of flower stems, number of pods plant^{-1}, above ground total dry mass at flowering and physiological maturity stages were decreased. Pod dry mass at physiological maturity decreased by 22.24% to 40.35% for different cultivars which clearly demonstrated the sensitivity of canola cultivars to increasing night/day temperatures.

By increasing the mean daily mean temperature from 12.5ºC (10/15ºC night/day) to 17.5ºC (15/20 ºC night/day) the duration of the period from planting to seedling emergence as well as the vegetative and reproductive growth stages were decreased. With the exception of the vegetative growth stage, GDD and PTU requirements to reach specific growth stages increased with an increase in temperature. Plant growth parameters such as dry mass, leaf area, number of pods plant^{-1} and pod dry mass plant^{-1} at specific growth stages showed a positive correlation with the number of days needed to reach that growth stage, but not with GDD or PTU requirements. Although the responses of cultivars to increasing temperatures did differ for most parameters measured, responses did not always correlate with the maturity grouping of cultivars, suggesting that responses to temperature may to a large extent be determined by the genetic make-up (breeding company) of cultivars.

These results indicate that number of days, GDD and PTU requirements to reach physiological maturity may be used to describe the cultivar maturity groupings, but because of the effect of temperature and day length, GDD and PTU should be more accurate.

UITTREKSEL

Canola se waarde as ekonomies belangrike akkerbou-gewas in Suid-Afrika het die afgelope aantal jare skerp toegeneem, omdat dit gebruik kan word om hoë kwaliteit kook-olie en margariene asook bio-brandstowwe en dierevoere, te vervaardig. In wisselboustelsels kan dit gebruik word om die siekte-ketting te breek en onkruidbeheer te vergemaklik. In hierdie studie is die invloed van temperatuur op die fenologiese reaksies van canola in terme van die aantal dae, gewasgroeidae en fototermiese eenhede, benodig om spesifieke groeistadiums te bereik, asook die invloed op groeitempo, vegetatiewe- en reproduktiewe groei onder gekontroleerde toestande nagevors.

Sewe canola cultivars vanuit die kort en mid-groeiseisoen volwassenheidsgroepe wat tans in die Weskaap verbou word is geplant in 3-liter plastiek houers gevul met ‘n 1:1 sand: kompos mengsel as groeimedium en besproei met ‘n volledig gebalanseerde voedingsoplossing met EC=2.0. Twee glashuise met nag/dag temperature van onderskeidelik 10/15^{o}C en 15/20^{o}C is vir hierdie doel gebruik. Die aantal dae, gewasgroeidae (GGD) en fototermiese eenhede (FTE) wat vanaf plant tot saailingverskyning; eerste volwasse blaarverskyning; eerste blomknop verskyning; eerste blom; saad verkleuring en fisiologies volwasse stadiums vereis word, is bepaal. Plant lengte is gemeet met 14-daagse tussenposes vanaf 28 tot 84 dae na plant. Plante is gemonster is tydens die eerste blomknopverskyning asook blom- en fisiologies volwasse stadiums om blaaroppervlakte (BO) en droëmassa (DM) te bepaal. Plant groeitempos (PGT) vanaf plant tot blomknopverskyning; blomknopverskyning tot blom en vanaf blom tot fisiologiese volwasse stadium is bereken. Relatiewe groeitempos (RGT) en netto-assimilasietempos (NAT), is bereken vanaf blomknopverskyning tot blom en vanaf blom tot fisiologiese volwasse stadium. Die aantal dae vanaf plant, asook GGD en FTE benodig om blomknopstadium, blomverskyning en fisiologies volwasse stadiums te bereik, is gekorreleer met BO en DM plant^{-1} asook die aantal peule en peulmassa plant^{-1} tydens genoemde groeistadia om moontlike verwantskappe te bepaal.

Die studie het getoon dat deur die nag/dag temperatuur te verhoog vanaf 10/15ºC tot 15/20ºC, plant lengte, aantal blare en BO plant^{-1} tydens blomknopverskyning, asook

PGT vanaf plant tot blomknopverskyning en RGT van blomknopverskyning tot blomstadium, toeneem. Daarteenoor het PGT van blomknopverskyning tot fisiologies volwassenheid, RGT van blom tot fisiologies volwassenheid, asook NAT van blomknopverskyning tot blomstadium en BO tydens blom en fisiologies volwasse stadium, afgeneem. Reproduktiewe ontwikkeling soos gemeet aan die aantal bloeistele, peule plant^{-1} en peulmassa plant^{-1} is ook benadeel deur genoemde verhoging in temperatuur. Die afname in peulmassa het gewissel tussen 22.24% en 40.35% vir verskilende cultivars en is ‘n duidelike aanduiding van die verskillende canola cultivars se gevoeligheid teenoor toenemende nag/dag temperature.

Die toename in gemiddelde nag/dag temperatuur vanaf 12.5ºC (10/15ºC) tot 17.5ºC (15/20 ºC) het die aantal dae vanaf plant tot saailing verskyning asook die vegetatiewe en reproduktiewe groei fases verkort. Met die uitsondering van die vegetatiewe groei fase, het die GGD and FTE vereistes om spesifieke groeistadiums te bereik toegeneem met ‘n toename in temperatuur. Plant komponente soos DM, BO, aantal peule plant^{-1} en peulmassa plant^{-1} tydens spesifieke groeistadia het ‘n positiewe verwantskap getoon met die aantal dae wat benodig is om spesifieke groeistadiums te bereik, maar sodanige verwantskap is nie bevestig met GGD en FTE vereistes. Hoewel die reaksie van verskillende cultivars teenoor ‘n toename in temperatuur vir die meeste gemete plantkomponente verskil het, het die reaksie nie altyd verband gehou met die volwassenheidsgroepering van die cultivars. Dit wil dus voorkom asof die reaksie teenoor temperatuur tot ‘n groot mate ook verband hou met die genetiese samestelling van die cultivar soos bepaal deur die telingsmaatskappy.

Hierdie resultate toon dat die aantal dae, GGD en FTE wat vereis word om fisiologiese volwassenheid te bereik gebruik kan word om die cultivar se volwassenheidsgroepering te beskryf maar dat GDD en FTE waarskynlik meer akuraat sal wees weens effek van temperatuur en daglengte op die ontwikkkeling van cultivars.

Acknowledgement

I hereby express my sincere gratitude to:

Almighty God who guided and preserved me throughout the study;

My study leader, Professor Andre Agenbag for his kind disposition, invaluable assistance and guidance throughout this study;

Professor Linus U. Opara of the Post-harvest technology department and Dr PJ, Pieterse; Department of Agronomy Stellenbosch University for their quality guidance from time to time during this study;

World Bank West African Agricultural productivity programme (WAAPP), for sponsoring the study;

My country, Nigeria and National Root Crops Research Institute (NRCRI) Umudike, for nominating me for the study;

My parents and siblings for their continuous prayers and moral support;

Staff of department of Agronomy at Stellenbosch University, especially Mr and Mrs la Grange, Dr Marcellous le Roux, Mrs Estelle Kempen, Mrs Simone Alexander for their great assistance and friendly disposition towards me during this study and especially Mr Nicke and Mrs Goosen for the quality time they spent assisting me in data collection.

Also Professor M. Kidd of the statistical consultation center at Stellenbosch University for always been there for me during my statistical analysis;

Finally Mr Yusuf Ras, the Liberian faculty of AgriScience Stellenbosch University.

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BD	budding
DAP	days after planting
DM	dry mass
FL	flowering
GDD	growing degree days
GS	growth stage
LA	leaf area
NAR	net assimilation rate
NFS	number of flower stems
NPPP	number of pods per plant
PDM	pod dry mass
PGR	plant growth rate
PTU	photothermal units
RCBD	randomized complete block design
RGR	relative growth rate
r-value	correlation coefficient of determination value

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CHAPTER 1

1.1 Introduction

Canola is increasingly becoming an important field crop in South Africa. Canola can be used to produce high quality cooking oil and margarine, animal feed, biofuel (Anonymous 2006) and in crop rotation systems to break the disease chain and improve weed management (Burton et al. 2008). In Canada, about 7.4 million ha of canola were grown in the great-plains province during 2009 (Statistics Canada 2010). In Australia two million hectares were sown to canola in 1999 but declined to half that due to drought in early years of this millennium. Recently it however recovered to 2.69 million ha in 2012 (Australian oilseed federation 2013). Canola is an oilseed crop and the first three letters “can” of its name were derived from Canada (the country of its origin), the fourth letter “o” was derived from oil while the two last letters “la” were derived from low acid, because its seed contains oil that has a low erucic acid content. Therefore it is defined as: an oil that must contain less than 2% erucic acid, the solid component of the seed must contain less than 30 micromoles of any one or any mixture of 3-butenyl glucosinolate, 4-pentyl glucosinolate, 2-hydroxy-3-butenyl glucosinolate and 2-hydroxy-4-pentyl glucosinate per gram of air-dry oil free solid (Anonymous 2006).

In Canada canola is planted in late April or early May, where-after it grows rapidly during the short summer season that has long warm days and is harvested at the end of September or early October. Although canola will flower much sooner at daylight lengths of 16 to 18 hours, it will eventually also flower at much shorter daylight lengths but after a longer period, (Kirkegaard et al. 2012). In South Africa and Australia canola is also planted in April or May but the growth take place during winter period, with daylight lengths of 9.5 hrs in May to 12 hrs in September and is harvested during October. The phenological development affects the success of canola production and is largely controlled by temperature (Morrison et al. 1992). Accurate timing of these phenological events is generally considered the most important factor determining crop adaptation and maximum yield in a particular environment (Fischer 1979, Richards 1991).

In general development of an annual crop from emergence to maturity can be divided into three major phenological developmental phases: emergence to flower buds

initiation-vegetative development, floral buds initiation to anthesis-reproductive development and anthesis to physiological maturity -seed filling (Craufurd and Qi 2001, Ritchie 1991, Siebert and Ewert 2012). However, canola developmental stages can be divided into six phases according to Harper and Berkenkamp (1975): Phase 0-Pre-emergency, Phase 1-Seedling, Phase 2-Rosette, Phase 3-stem elongation, Phase 4-flowering, Phase 5-Seed maturation. Under climate change scenarios, increase in both the mean and extremes of temperature are expected for many parts of the world (IPCC 2001). These changes can impact largely on the growth and phenological development of crops. Temperature, and to lesser extent photoperiod, have been reported to be the major environmental factors that determine the timing and duration of each of the phenological phases (Roberts et al. 1993). Many models have been developed to explain the phenological phases that take place during growth and development of crops (Alocija and Ritchie 1991, Matthews and Hunts 1994), while the physiological mechanisms that govern the transition from one phenophase to another are strongly influenced by environmental factors and have been described using photothermal models (Summerfield et al. 1991).

Photoperiod has been reported to be the principal factor that determines the time of floral initiation and hence anthesis in many crop species (Burtero et al. 1999). Photoperiod, for example affects floral development of rice (*Oryza sativa* L.) (Coolhaas and Wormer 1953), caryopteris (Piringer et al. 1963), wheat (*Triticum aestivum* L.) (Slafer and Rawson 1994), barley *(Hordeum vulgare* L.) (Kernich et al. 1996) and quinoa (*Chenopodium quinoa willd*) (Burtero et al. 1999). However, it is not clear whether the duration of the reproductive phase is affected directly (immediate response) by the photoperiod experienced during this phase or indirectly (delayed response) by the photoperiod experienced in earlier developmental phases. The delayed effects on reproductive development could be because of the fact that more leaf primordia are formed under an extended duration of the vegetative period and this means that anthesis is delayed since more leaves have to appear and all the leaves must have emerged before anthesis will occur (Kiniry et al. 1992). The underlying assumption here is that the total leaf number cannot be altered after the end of the vegetative growth phase by transfer conduct during anthesis and seed filling. However, Slafer and Rawson (1995) and Kernich et al.(1996) have shown that time from the end of leaf appearance to

anthesis is affected by the photoperiod after floral initiation, but not leaf number in wheat and barley.

Ritchie and Smith (1991) reported that temperature regime is a major factor controlling the rate of leaf appearances. Hence “phyllochron” is defined as a constant interval of thermal time between successive leaves appearance. However the effect of temperature on the time interval between successive leaves’ appearance (phyllochron) is crop specific for the different field conditions (Cao and Moss, 1989). For chenopodium, photoperiod was reported to decrease the ‘’plastochron” (the time between initiation of two successive primordia) with transfers from inductive to marginally or vice versa (Thomas, 1961). A photothermal duration effect on seed maturation processes has been demonstrated for soybean (*Glycine max* (L) *merril*), peanut (*Arachis hypogeal L*), bambaranut (*Vigna subterrenea* (L) *verdc*), rice (*Oryza sativa*), muccuna spp, maize (*Zea mays L*), sorghum (*Sorghum bicolor*) and field pea (P*isum sativum*) (Bagnall and King, 1991, Birch et al 1997, Craufurd and Qi 2001, Craufurd et al. 2003, Linnemam 1993, Morandi et al. 1998, Poggio et al. 2005 and Qi et al. 1998,). It has also been reported that photothermal regime influence the vernalisation sensitivity of crops. Plants vernalised for 50 days showed greater response to photoperiod than those vernalised for 15 days. As the duration of stem enlongation lengthened in photoperiod-sensitive cultivars by exposure to less inductive photoperiods, a higher number of fertile florets at anthesis is produced, leading to an increased grain number and thereby to higher yield (Gonzalez et al. 2003). The knowledge of timing of phenological events in crops is very important for optimal agronomic practises and breeding programs, and also for crop-growth modeling and specific environmental adaptation (Saarikko and Carter 1995).

1.2 Problem statement

The timing of leaf emergence, flowering and seed filling, as influenced by photothermal exposure and duration are critical factors in crop production, especially in the mediterrenean environment with its characteristic period of increasing temperatures and water stress that occur towards the end of the growing season. This has been extensively studied on other cereal crops, as highlighted earlier in this introduction, but because canola is a relatively new crop in South Africa no such study has been

conducted on canola. It is therefore very important that this study is conducted on canola to maximally exploit its productive potential.

1.3 Aims/Objectives

The knowledge generated from this study will greatly enhance agronomical management of canola and also serve as a tool for canola breeding for South African conditions. It will also provide information with regard to the production potential in new production areas and the possible responses of cultivars to planting dates. Results will also give an indication of possible impacts of rising temperatures due to climate change.

Hence the objectives of this study were:

To determine the phenological responses of canola cultivars to different temperature regimes

To evaluate the effect of different temperature regimes on growth and yield of canola cultivars

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CHAPTER 2

Literature Review

2.1 Environmental adaptation of crops

Many climatic and soil factors such as; rainfall, altitude, day length, light intensity, temperature, humidity, wind speed, soil type, soil nutrient content and soil pH affect crop adaptation to a particular environment. However, day length (photoperiod) and temperature are key role players in shaping the major biomass production of the world and determining their distribution to a specific environment across the globe. For example, the pattern of distribution of leave area index (LAI), which is one of a crop's most important growth and yield parameters has been reported to be driven by temperature and photoperiod (Breda, 2008). Canola/Rapeseed has been reported to show response to temperature and photoperiod in such manner that pre-bud appearance (vegetative growth stages) phenology is controlled by temperature and photoperiod depending on the cultivar, while, post-bud appearance (reproductive growth stage) phenology is controlled by temperature alone, (Hodgson, 1978). Hartel (2012) reported that variation in phenophase duration in the field of annual wheat and rapeseed cultivars were accounted for by their correlation with temperature and photoperiod.

Many other studies have been conducted to investigate the impact of mean and extreme temperatures on crop environmental adaptation and yield stability, especially in view of the climate change scenarios (Wheeler et al. 2000, IPCC 2001a, Mckeown et al. 2005). The impact of mean and extreme temperatures varied geographically, and depended upon the simulated genotypic properties (Challinor, et al. 2003). Temperature stress is perhaps the most complex and least accurately quantified of the processes that affect crop development. Therefore, genotypic differences in tolerance to temperature stress have been documented in many annual crops.

Craufurd et al. (2003) screened 22 genotypes of groundnut using controlled environments in order to identify genotypes that were tolerant to high temperature stress, at flowering or at micro-sporogenesis (3 days before flowering) and the results showed 6 genotypes of diverse origin that were heat tolerant. Challinor et al. (2007)

used detailed information from the above mentioned genotype screening study to properly investigate the extent of genotypic adaptation to high temperature stress associated with climate change, within the current crop germplasm. Their findings suggested that changes in mean temperature, through their impact on crop developmental rates, may have a widespread effect on crop adaptation and productivity.

Similarly, both Curtis (1968b) and Andrews (1993) concluded that homeostasis of a crops' environmental adaptation is probably determined by phenological responses to the photothermal regime. Craufurd and Qi (2001), found that genotypes exhibit variation in photoperiod-sensitivity and minimum duration from basic vegetative phase to panicle initiation and flowering of sorghum and concluded that these were the major determinants of sorghum adaptation to tropical climate of West Africa.

2.2 Phenological responses of crops to temperature

Crops develop from seed germination to fruit or seed maturity by going through different phenological phases of development, which can be defined morphologically, but are not independent of each other. Hence, the development of each phenological phase (phenophase) is affected by the activities or rate of development of previous phase(s) (Saarikko and Carter 1995). The physiological processes that govern the transition from one phenophase to another are strongly influenced by environmental factors. Many models have been proposed to relate environmental factors to the phenological development of crops (Ritchie 1991, Summerfield et al. 1991, Robbertson 1993). Of all the environmental factors, the most influential on crop phenological development, besides rainfall, is temperature, such that many crop simulation models correlated the rate of development during most of the phenophases to temperature, (Angus et al. 1981, Ritchie 1991, Summerfield et al. 1991. Slafer and Rawson 1994). Slafer (2003), Mcmaster et al. (2008) and Luedelling et al. (2009) reported that the phenological development rate and yield of plants are mainly determined by genetically prescribed responses to temperature.

Chmeilewski et al. (2004) reported that increased mean temperature and decreased photoperiod caused a shortening of developmental phases of annual crops with effects on crop yields. The shortening of growing season results in less absorbed radiation and

therefore less biomass accumulation and yield. Although, the general responses of crops increasing temperatures in the study above were similar, the magnitude of the responses differs between crop species. Similarly, Fitter and Fitter (2002) in their multi-species study, investigated the rapid changes in flowering time of 385 British plants. It was discovered that for species flowering in spring days (February, March and April), the first flowering date was 4 days earlier for each degree (^{o}C) increase in temperature of the previous month.

In another multi-species study, Pearson correlation coefficients were used to test for relationships between minimum temperature and average first-flowering dates. It was found that advance of flowering date in 89 species are directly correlated with a local increase in minimum temperature in Germany (Abu-Asab et al. 2001). Also, Shleip et al. (2009) in their multi-species study using the Bayesian analysis approach, reported that there were differences among the phenological groups sensitivity to temperature increase and the time period of the analysis. They reported that phenophases which occur in April and May were responding mainly to April temperatures, but not as much to March temperatures. Therefore, their results, indicate that plants with different sensitivities to temperature changes according to the time of the year and that phenophases which show a prompt temperature response pattern can be distinguished from those that show a delayed response pattern.

Siebert and Ewert (2012) reported that the length of growing season of oats in Germany has been reduced by about two weeks between 1959 and 2009 as a result of earlier occurrence of phenological events. The thermal sensitivity of maize cultivars has been expressed as the increase in number of leaves produced per hour of photoperiod in excess of 12.5hours or thermal duration of the photoperiod-sensitive interval prior to tassel initiation and to this, Birch et al. (1997) reported the value ranged from 0.3 to 1.5 leaves h^{-1} or 5.0 to 27.3 degree days using optimized base, optimum and maximum temperatures.

Many studies in a controlled environments where every other environmental factors were kept optimum have revealed that temperature plays a key role in determining the developmental rate and yield of crops and especially dry matter production and assimilate accumulation and distribution across the crop’s vital organs during different

growth stages (Ohe et al. 2007, Thomas et al. 2010, Ambardekar et al. 2011, Kim et al. 2011).

2.3 Effect of temperature on seed germination

Canola seed germination, like every other seed, is affected by a number of factors, including; seed viability, seed size, soil moisture and microorganisms, soil air (oxygen) and temperature. The stepwise processes of seed germination starts with water absorption, activation and synthesis of enzymes, breakdown of stored food in the seed, transport of breakdown products within the embryo and then initiation of embryo growth. All of these processes are biochemical in nature and are temperature sensitive reactions, except water absorption (Mendham and Salisbury 1995). Various studies have shown that canola seed can germinate at a constant temperature of 2^0C, however, sustained low temperatures have been reported to cause damage to the seed, embryo which reduces germination and growth (Daniels et al. 1986, Williams et al. 1987, Bouttier and Morgan 1992).

Similarly, Dhawan (1985) reported that cold soils, <5^{o}C at seeding and 2 weeks thereafter, can increase the canola seed mortality rate by 10% to 20%. Generally, temperatures below 10^{o}C have been reported to result in progressively poorer germination of canola seed and cultivars and seed lots differ in their ability to germinate in low temperatures (Christensen et al. 1985). Days to 50% germination for canola seed based on how many growing degree days (GDDs) accumulated from planting date have been reported as 75 to 120 GDDs for all temperatures from 3^{o}C and above for B. napus and 115 GDDs for *B. rapa* at temperatures above 8^{o}C (Vigil et al. 1997). Similarly, the germination rate of *Brassica napus* seeds was reported to decrease with a decrease in temperature from 25^{o}C to 5^{o}C (Witcombe and Whittington 1971). While, germination of Cabbage and *Brassica hirta* seeds was reported to occur at a temperature as low as O^{o}C, if the soil moisture is still in the liquid state (Coffman, 1923).

Seeds from other crops exhibit similar responses to a wide range of temperature and day length regimes in their ability to germinate (Torfason and Nonneck 1957, Peser 1970, Baskin and Baskin 1971, Dickson 1971, Buxton and Sprenger 1976, Littlejohus and Tanner 1976, Villalobos and Ritchie, 1991). For example, seeds of *Verbascum*

bladaria L was reported to germinated up to 100% in darkness over a wide range of incubation temperatures during summer (Baskin and Baskin 1981), while seeds of *Lamium amplexicule* germinated from 70-100% in darkness at 15/6^{o}C in January and February, but only 0 to 25% during the rest of the year. Hence, Baskin and Baskin (1983) concluded that, the temperatures required for germination in darkness are higher than those that occur in the field during winter. Holm (1972) reported that germination of buried seeds of *Ipomea purpurea* L, Roth, *B. kaber* (DC) was inhibited by decreased oxygen levels and presence of volatile metabolites. Acharya et al. (1983) screened different genotypes of canola on the basis of their ability to germinate at low temperatures and found that *B. rapa* was better adapted to low temperatures than *B. napus*

2.4 Effect of temperature on vegetative growth of crops

The vegetative growth phase of canola is characterized by leaf appearance and expansion. Leaf expansion rate (LAX) and leaf area duration (LAD) of canola are strongly affected by air temperature (Morrison et al. 1992). Canola also shows sensitivity to photoperiod from emergence to the end of the vegetative growth phase, in such a manner that the duration of vegetative growth phase is shortened by long days, while short days delayed the rate of leaf appearance at the beginning of the vegetative growth phase (Nanda et al. 1996).

Temperature on the other hand controls the duration between germination, emergence to the end of vegetative phase and from stem elongation to mid flowering stages (Gabrielle et al. 1998). The rate of growth in each of these stages is hastened by increasing temperature, when other growth limiting factors are at an optimum (Morrison et al. 1989). However, Nanda et al. (1996) reported that the effect of temperature on the duration of the vegetative growth phase of canola is not the rate of leaf appearance, but the difference between the sowing date and first real leaf appearance. For this reason the appearance of the first real leaf was delayed by 1.35 days for each 1^{o}C decrease in temperature. Similarly, Morrison et al. (1991) reported that the final canola leaf number is also effected by temperature and photoperiod, to such an extent that the crop produced less leaves when it was exposed to low temperature during long days and vice versa.

Differences among canola varieties on average rate of leaf appearance have been observed by Kasa and Kondra (1984) who reported that a new leaf appears every 2.33+0.007 days for *B campestris* and 3.18+0.08 days for *B. napus* cultivars. Similarly, Nanda et al, (1996) reported that there were differences among canola cultivars with regard to their final number of leaves. Those that have intrinsic earliness (in terms of maturity) produced less leaves than those with intrinsic lateness.

Effect of temperature and photoperiod on the rate of leaf appearance has also been established for other field crops (Morandi etal, 1988, Ritchie and Ne Smith, 1991, Villalobos and Ritchie 1991), to such an extent that when a crop is subjected to low temperatures during early developmental stages, it will experience an increased rate of leaf appearance at the vegetative growth (Rawson and Dunstone 1986, Cao and Moss 1989).

2.5 Effect of temperature on reproductive growth of crops

The principal objective in canola production is to choose cultivars that will flower at a time, which will enable seed development to be completed before the onset of severe frost, high temperatures and/or drought stress (Robertson 2002). The reproductive growth stage of canola starts from bud initiation to 40% seed moisture content (Edward and Hertel 2011). Cultivar, temperature, photoperiod and vernalisation requirement interact to determine time to flowering of canola (Mendham and Salisbury 1995).

Many authors have reported that the reproductive growth stage of canola was not responsive to photoperiod (Hoddgson 1978, King and Kondra 1986, Robertson et al. 2002, Hertel 2012), but, photoperiod did influence time to flowering through its delay or hastening effect on the vegetative stage. Canola is a known long day plant and increased day length up to 16h has been reported to significantly reduce the number of days to flowering, while further increases to 20h had no effect on days to flowering (King and Kondra 1986). Satisfying vernalisation requirement has been reported to significantly reduce the growing degree days or thermal time of the canola reproductive growth stage (Robertson 2002). Similarly, Angadi et al. (2000) reported that the effect of vernalisation on time to flowering was such that the absence of vernalisation, in relatively high temperature ranges of 18-20^{o}C, may sometimes result in crops that

remain vegetative, without bud initiation. Robertson (2002) reported that time to flowering of canola crop decreased with an increase in temperature, up to 20^{o}C, yet subsequently increases with further increase in temperature. Therefore, according to this author, the optimum temperature for canola is around 20^{o}C.

Differences in response of the reproductive growth phase to temperatures among canola cultivars has been established, for example, Robertson et al (2002) reported that duration of the reproductive phase varied from 33-50 days at 18^{o}c, while time between visible buds and flowering varied from 9 to 11 days among 21 cultivars of two genotypes (*B. napus* and *B. campestris*). Salisbury and Green (1991) also found that when vernalisation requirement is not met, the early maturing cultivars showed the strongest response to temperature with regard to time to flowering. In contrast to these, late maturing cultivars showed the largest response when the crop is vernalized.

These results corroborate proposals that there is great interaction between photoperiod and temperature in determining the duration to flowering between crops. Therefore, it seems that if a crop is a short day plant, high temperature will reduce the duration of the flowering time during short days, while low temperature will induce some dormancy and thereby increase the time to flowering. Also, when a long day crop is exposed to high temperature in combination with short days, floral bud formation is delayed, but if a long day crop is exposed to long day conditions in combination with high temperatures the time to flowering will be reduced.

2.6 Effect of temperature on grain yield and quality

The knowledge of environmental factors affecting both grain number and grain weight determination is key to understanding grain yield in crops. Many of the physiological processes affecting crop growth and development are controlled by temperature (Wheeler et al. 2000, Ghaffari et al. 2002, Southworth et al. 2002). While, pre-floral induction is affected by daylength, post-induction phase has been reported to be solely controlled by temperature (Heatherly and Elmore 2004). Lower grain yields often reported at higher temperatures have for this reason been attributed to the reduction of the crop growing period (Tubiello et al. 2007). Crop phenology advancement is known

to shorten the period for canopy development, therefore, affecting radiation interception, biomass accumulation and the grain-filling period (Kristensen et al. 2011).

The response of canola yield in North India to the rising seasonal temperature varies depending on the locations. Hertel (2012) stated that the rate of oil and yield accumulation of canola at Gilgandra and Wellington in Australia is strongly correlated to thermal time. A reduction in grain yield of 4 to 5% for each $1^{o}C$ increase in mean temperature for England and Spain has been reported (Wolf et al. 2002).

Furthermore, oil concentration in canola (B. napus L.) has been reported to be determined during seed filling period and variation in oil concentration is closely related to temperature during that period. For instance, Faraji (2012) reported that there was a negative linear relationship between air temperature during seed filling period and oil concentration in both open pollinate and hybrid genotypes of canola. He further stated that high temperatures increased the rate of plant development thereby shortening the seed filling period and reducing the oil concentration potential of all the canola cultivars he investigated. Similarly, Omidi et al, (2010) reported that a prolonged high temperature during the seed filling stage resulted in the production of low quality seed and reduced the oleic acid content. However, at maturity high temperature rather increased oleic acid and decreased linoleic acid content of canola seed, a situation that was reversed at low temperature (Lagravere et al, 2000). Therefore, Robertson et al, (1978) reported that canola seed oleic acid content is thus correlated to temperature during the period of 21 to 70 days after flowering.

2.7 Effect of temperature on biomass accumulation and allocation

The impact of increased temperature on biomass accumulation can be both positive and negative, because it may increase photosynthesis if it is below the optimum temperature, but reduce total biomass accumulation by shortening the crop growth period (Porter and Gawith 1999). An increase in especially night temperature study findings were established already reduced crop biomass accumulation by increasing the respiratory rate and consequently increase the rate of oxidation of the accumulated biomass (Schlenker and Roberts 2009). Increased temperature above the optimum range has also been reported to cause heat stress on some grain crops (Lele, 2010). On

the other hand, increased temperature can positively impact on crop biomass accumulation by stimulating vegetative growth (Lobell, 2007) and increasing the photosynthetic rate (Turnbull, et al, 2009).

Dry mass partitioning is dynamic, depending on the prevailing relationship between sinks and sources at low and high temperatures and is also regulated by the level of saccharose (Thomas et al. 2010). Understanding allocation of resources, including photosynthate source-sink relationships of canola plants, is important because these relationships influence yield (Freyman et al. 1973). Rood et al. (1984) investigated the changes in photosynthate source-sink relationships in canola (B. campestris L cv. 'Span') using $^{14}CO_2$. They observed that at flowering, leaves and stem were the main sites of assimilation taking up to 46% and 41% of the $^{14}CO_2$, while pods assimilated only about 5%. At the onset of pod filling, leaves, pods and stems assimilated 19%, 32% and 43% respectively, while, at onset of seed ripening, they took up 17%, 46% and 29% respectively. Seeds were the main sinks during pod filling and ripening. Similarly, Major et al. (1978) reported that when rapeseed plants were allowed to assimilate $^{14}CO_2$ through different plant parts, lower leaves allocated to the roots, while upper stems and leaves distributed mainly to seeds and pods. Xu and Zhou (2005) showed that dry mass and ^{14}C produced in leaves were allocated into roots under water stress, but increased night temperature reversed allocation to roots and were allocated to leaves.

2.8 Effect of temperature on plant radiation use efficiency

The magnitude of crop responses to temperature regimes can also be measured by physiological determinants such as the efficiency for converting radiation into biomass production and biomass partitioning to reproductive organs (Passioura 1996). Under high temperature conditions, the loss in crop productivity is mostly related to decreased assimilatory capacity as a result of reduced photosynthesis due to negative impact of above-optimum temperatures on membrane stability and enhanced respiration (Sinsawt et al. 2004, Hay and Porter 2006, Barnabas et al. 2008). The consequence of these responses is a reduced crop radiation use efficiency (RUE) and biomass production per unit of light intercepted by the canopy, as has been reported for wheat (Reynolds et al. 2007) and maize (Cicchino et al. 2010). Similarly, Edreira and Otegui (2012) reported that exposing temperate and tropical maize hybrids to above-optimum temperature

during grain filling caused large reductions in RUE and harvest index (HI). Similarly, suboptimum temperatures also have effect on crop RUE. For instance, Louarn et al. (2007) identified cold temperature as the main reason for a decline of RUE in maize crop which led to reduced biomass production.

Conclusions

In view of global warming due to climate change, temperatures of most regions of the world are increasing (IPCC, 2007). Therefore, temperature may become the most important environmental factor regulating crop growth and production potential. From the literature it became clear that temperature singularly, but also in conjunction with day length affects all growth processes of crops, but crops and even different cultivars of the same crop may differ in their response. Canola is a relative new crop in the RSA and all cultivars planted are imported from Australia. Little is known about the responses of specific cultivars and maturity groups to local temperature regimes as well as in relation with day length. Such information will be needed to predict how different cultivars (maturity groups) will perform when planted at different planting dates and in different production areas.

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CHAPTER 3

Materials and methods

3.1 Study design

The experiment was laid out as a randomized complete block design (RCBD) with two temperature regimes and seven canola cultivars as treatments. Four replications were used and individual plants represented an experimental unit. Provision has been made for three sampling times.

3.2 Plant material and growth conditions

Seven cultivars of canola, Hyola 571 CL, AGAMAX, 45Y86, 44Y84, Hyola 50, 43Y85, and Hyola 575 CL were planted (four seeds per 3 litre plastic bags filled with the mixture of sand and compost at ratio of 1:1 and irrigated with fully balance nutrient solution at 2.0 EC) in two glasshouses. The cultivars were selected based on the duration of their maturity. For instance, 45Y86 and Hyola 50 are mid-maturing cultivars; 44Y84 is mid-early, while, 43Y85, AGAMAX, Hyola 571 CL and Hyola 575 CL are early maturing cultivars. During the seedling stage, plants were thinned to one per bag. The two temperature regimes were set at 15/20^{o}C and 10/15^{o}C night/day temperatures respectively. The plants were irrigated twice a day to re-fill the bags to field water capacity.

Daylight length (number of hours of sunshine) was obtained from the South African weather service (http//www.Weathersa.com). Crops were planted on 11 February 2014 and the final harvest was done on 14 July 2014 with the result that the day length varied between 13:20 hours at planting and 10:48 hours during the final harvest. The light intensity within the glasshouses as well as outside exposed environment, were measured weekly at 12h00, from the seedling stage of the plants and averages of 211.6 µmol m^{-2} s^{-1} for 15/20^{o}C glasshouse, 249.1 µmol m^{-2} s^{-1} for the 10/15^{o}C glasshouse and 481.5 µmol m^{-2} s^{-1} for outside environment were obtained. Temperature loggers were put in each glass house to record the actual temperature of the glasshouses to make sure that the set temperatures were achieved.

3.3 Data recorded

The number of days required to reach the following growth stages (GS) according to Harper and Berkenkamp (1975) were recorded: Seedling stage (GS 1.0); first true leave (GS 2.1); visible inflorescence at center of rosette or budding (GS 3.1); first flower open (GS 4.1); beginning of seed filling (GS 4.4); lower pods filled to full size and become translucent (GS 5.1); and seeds in lower pods turn brown which is physiological maturity (GS 5.4). Number of days was multiplied by the mean of the set night/day temperatures 17.5^{o}C for 15/20^{o}C and 12.5^{o}C for 10/15^{o}C to calculate the growing degree days (GDD).

The growing degree days (GDD) x mean daylight length (sunrise to sunset) was used to compute the photothermal units (PTU) needed by different cultivars to reach the above described growth stages. Plant height was measured at 28, 42, 56, 70 and 84, days after planting (DAP). Before budding it was done from the base of the soil stem at soil level to the tip of the tallest leave), but after budding, it was measured to the tip of the flower bud. Plants in both glasshouses were sampled at the budding, full flowering and physiological maturity stages to determine the leaf area and dry mass, oven dried for 48hrs at 80^{o}C. Number of flower stems (NFS) and pods (plant^{-1}) (NPP) were recorded at final harvest (physiological maturity) stage and pods dry mass (PDM) (plant^{-1}) were also obtained after oven drying the samples for 48hrs at 80^{o}C. Formulae described by Paine et al. (2012) were adopted to calculate the following plant growth parameters for different cultivars and temperature regimes. Plant growth rate (PGR) from planting date to budding, from budding to flowering and from flowering to physiological maturity were calculated by dividing the difference between the dry mass at beginning(DM_1) and at the end (DM_2) of each growth interval with the number of days needed for the different growth intervals. Relative growth rates (RGR) were calculated by dividing each PGR with DM1 while net assimilation rates (NAR) were calculated by dividing PGR with leaf area at the beginning of each growth interval (LA_1). Relative growth rate (RGR and net assimilation rate (NAR) were only calculated from budding to flowering and from flowering to physiological maturity, because the plants did not have any leaf area at planting and seed mass at planting are so small that RGR values would be unrealistic. Because of large differences between plants, only mean values; and not individual replication values were used. DAP, GDD (degree-days) and PTU (degree-hour-days) at budding, flowering and physiological maturing stages were correlated with LA, DM, NPP and PDM at budding, flowering and physiological maturing stages to determine whether there were relationships between the variables.

3.4 Data analysis:

An appropriate analysis of variance (ANOVA) was performed, using Statistica software, version 12®. The Bonferroni test's least significant difference (LSD) values were calculated at the 5% probability level to compare treatment means.

References

Harper FR, Berkenkamp B. 1975. Revised growth key for Brassica Campestris and B. Napus. *Canadian Journal of Plant Science 55: 657-658*.

Paine CET, Matthews TR, Vogt DR, Purves D, Rees M, Hector A, Turnbull LA. 2012.''How to fit nonlinear plant growth models and calculate growth rates: updates for ecologists". *Methods in Ecology and Evolution* 3:245.

CHAPTER 4

Effect of temperature on morphological development of seven canola cultivars.

Results and discussion

All measured plant components were analyzed statistically, but only those that have shown significant differences at P=0.05 were presented and discussed.

4.1 Plant height

Plant heights were measured at 14-day intervals and statistical analysis was done on the data sets of 28, 42, 56, 70 and 84 days after planting (DAP). Because of a significant cultivar x temperature x measuring date interaction, no main effects or cultivar x temperature interaction were presented or discussed.

As expected all cultivars showed a significant increase in plant height with time (days after planting) and heights of about 150 cm were achieved after 84 days when plants were already in the pod filling stage (Figure 1). Cultivars responded differently to temperature treatments. Cultivars, 43Y85, 44Y84, Hyola 575 and Hyola 50 showed little response to the different temperature treatments (10/15^{0}C and 15/20^{0}C), but all other cultivars showed a significant increase in plant height with an increase in night/day temperature from 10/15^{0}C to 15/20^{0}C. Differences in plant height were in most cases shown from 56 DAP onwards and the largest differences were found with early and mid-(early) maturing cultivars Hyola571 and AGAMAX and 43Y85 because these cultivars were already at the budding stage, which is characterized by rapid stem elongation. Because early maturing cultivars such as 43Y85 and Hyola 575 did not show a large response to temperature, no conclusion can be drawn with regard to the response for different maturity groups.

These results are in agreement with the findings of Qaderi et al. (2006) who reported that higher temperatures increased height of canola plants, but Dong at al. (2011) reported that in rice, higher temperatures in combination with short day lengths reduced stem height in rice crop in eastern China.

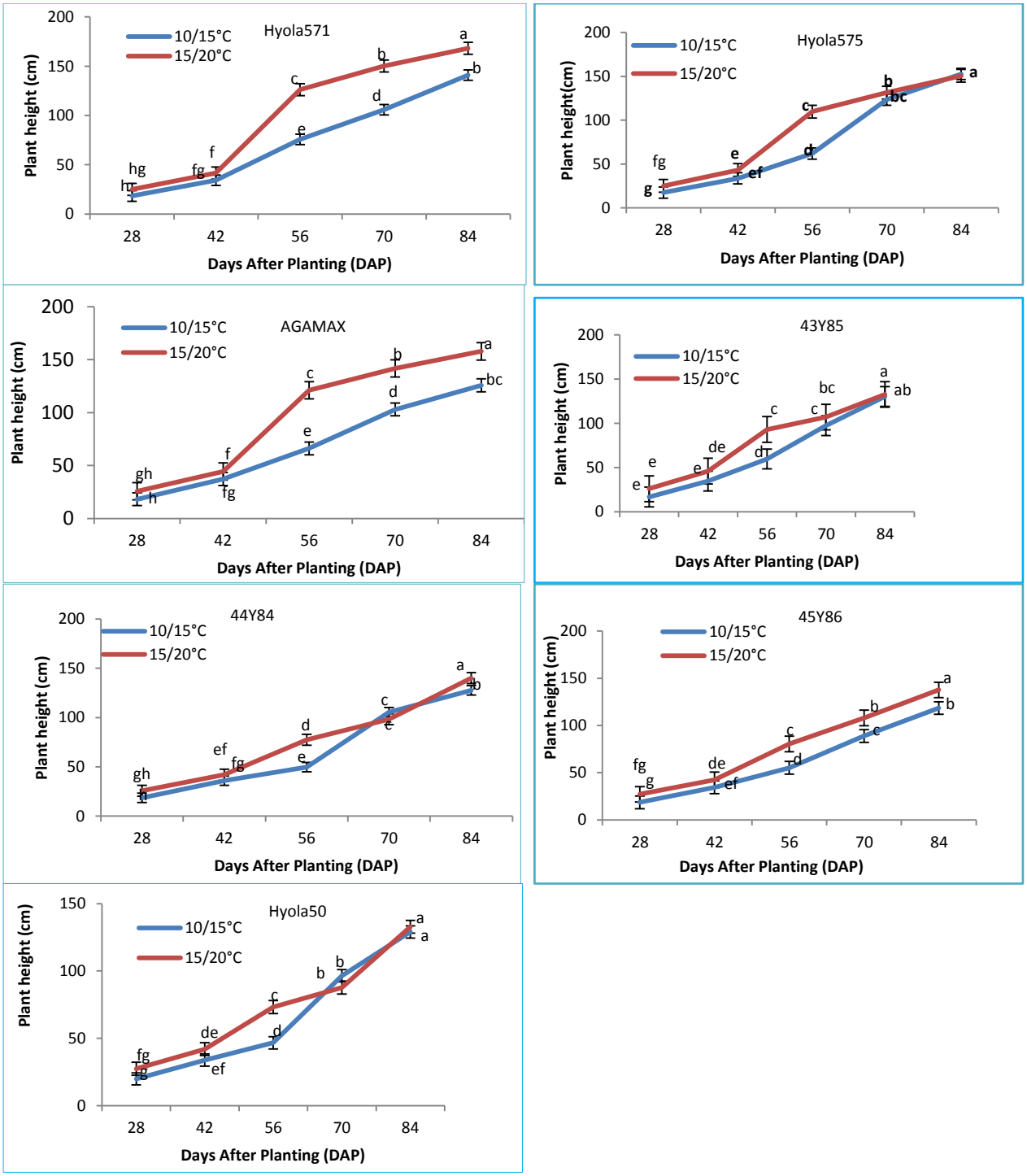

Figure 1 Plant heights (cm) of different canola cultivars, measured at 28, 42, 56, 70 and 84 days after planting (DAP), in response to night/ day temperatures of 10/15^{0}C and 15/20^{0}C. *Values with the same alphabetical lettering do not differ significantly at P=0.05*

4.2 Number of leaves

The total number of leaves (plant^{-1}) was counted after the end of the vegetative stage when budding started (growth stage 3.1) and ranged from 10 to 14 leaves per plant.

Cultivars did differ with regard to the number of leaves produced when subjected to different growing temperatures (Figure 2). In general cultivars tend to produce more leaves at the higher night/day temperature (15/20^{0}C), but with the exception of the early maturing cultivar 43Y85 and the mid maturing cultivar 45Y86, differences were not significant. At the lower temperature regime (10/15^{0}C), early maturing cultivars Hyola 571 and Hyola 575, produced significantly less leaves than other cultivars. At the higher temperature regime of 15/20^{0}C, Hyola 571, Hyola 575 and AGAMAX produced less leaves than cultivars 43Y85, 44Y84 and 45Y86. Hyola 571 and Hyola 575 also produced less leaves than Hyola 50. Hyola 50 on the other hand, produced less leaves than early maturing 43Y85 and mid-early 44Y84 and mid maturing 45Y86. Because cultivars 43Y85, 44Y84 and 44Y85 tend to produce the largest number of leaves at especially the higher temperature regime, results suggested that number of leaves produced before budding stage when stem elongation started, may to a larger degree be related to the cultivar's origin (breeding company) than maturity grouping.

These results are in contrast to the findings of Slauenwhite and Qaderi (2013) who found no significant difference in leaf numbers (plant^{-1}) among four canola cultivars; 46A76, 45H72, 45H24 and 45H21 grown at day/night temperature regimes of 24/20^{0}C and 30/26^{0}C, though we don't know the maturity grouping of these cultivars. These authors also reported that higher temperature reduced leaf number per plant. This contrasting results may indicate that the lowest temperature regime of 24/20^{0}C used in their study were already above the optimum for leaf initiation in canola.

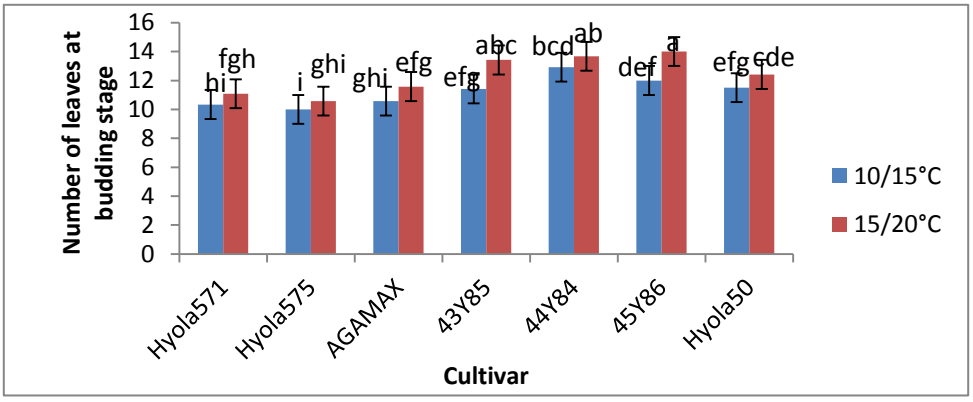

Figure 2 Number of leaves (plant^{-1}) of different canola cultivars, measured at the beginning of budding (growth stage 3.1) in response to night/ day temperatures of 10/15^{0}C and 15/20^{0}C. *Values with the same alphabetical lettering do not differ significantly at P=0.05*

4.3 Leaf area

Leaf area (cm^2 $plant^{-1}$) was measured at budding stage (growth stage 3.1), flowering stage (growth stage 4.1) and during the final harvesting when pods were physiological matured (growth stage5.4). In general leaf area $plant^{-1}$ increases from budding stage to reach a maximum at flowering, where-after it started to decrease.

At all sampling stages, leaf area (cm^2 $plant^{-1}$) was affected by temperature regime, with on average, larger leaf areas produced at the lower night day temperature of $10/15^0C$, during sampling at flowering and at final harvesting stage (Figure 3), but not so at budding stage. This tendency indicates an increase in leaf senescence at the higher temperature regime. Different canola cultivars, however, responded differently to the increase in temperature from $10/15^0C$ to $15/20^0C$.

At budding stage only Hyola 575 and Hyola 50 showed a significant increase in leaf area (cm^2 $plant^{-1}$) with an increase in temperature (Figure 3a), compared to early maturing Hyola 571 at the higher temperature regime ($15/20^0C$), but not so at the lower temperature regime ($10/15^0C$). Although Hyola 571 showed, on average, the smallest leaf area (cm^2 $plant^{-1}$) at budding stage, no clear trend due to maturity grouping was shown.

At flowering stage, significant decreases in leaf area (cm^2 $plant^{-1}$) due to the increase in temperature from $10/15^0C$ to $15/20^0C$ were shown for cultivars, Hyola 571, AGAMAX and 45Y86, while 43Y85 was the only cultivar to show a significant increase in leaf area with an increase in temperature regime (Figure 3b). Cultivar AGAMAX produced the largest leaf area (cm^2 $plant^{-1}$) at the low temperature regime ($10/15^0C$), while at the higher temperature regime ($15/20^0C$), the leaf area of 43Y85 plants at flowering were significantly larger than that of all other cultivars tested. On average, early maturing cultivars Hyola 571 and Hyola 575 tend to produce the smallest leaf area (cm^2 $plant^{-1}$.)

During the final harvest at growth stage 5.4, leaf area (cm^2 $plant^{-1}$) with the exception of the early maturing cultivar Hyola 571 tend to decrease with an increase in temperature regime, but differences were not significant (Figure 3c). No significant differences were recorded between cultivars at the $10/15^0C$ temperature regime, but at the higher temperature regime ($15/20^0C$), Hyola 575 showed a significantly smaller leaf area compared to 44Y84. In general mid-early maturing cultivars tend to have larger leaf areas than early maturing or mid maturing cultivars at this stage.

These results did not show clear evidence that cultivars of the same maturity group followed a similar pattern with regard to their leaf area development at any of the sampling dates, but in general, mid-early maturing cultivars tend to produce the largest leaf area(cm^2 $plant^{-1}$). Higher night/day temperatures resulted in larger leaf areas at budding, but smaller leaf area at flowering and especially during the final harvesting at growth stage 5.4. Schwabe (1957) and Humphries (1969) also showed that leaf initiation

and expansion rate during the early growth stage of seedlings were increased by higher temperatures. Rawson and Dunstone (1986) as well as Nanda et al., (1995) reported that temperature effects crop phenology and thus can change the pattern of leaf area development by altering the source-sink relationship. They observed that before onset of flowering, leaves and stem were the main sites of assimilation, taking up to 46% and 41% of dry matter respectively, but at the onset of pod filling, leaves assimilated only 19% of dry matter produced.

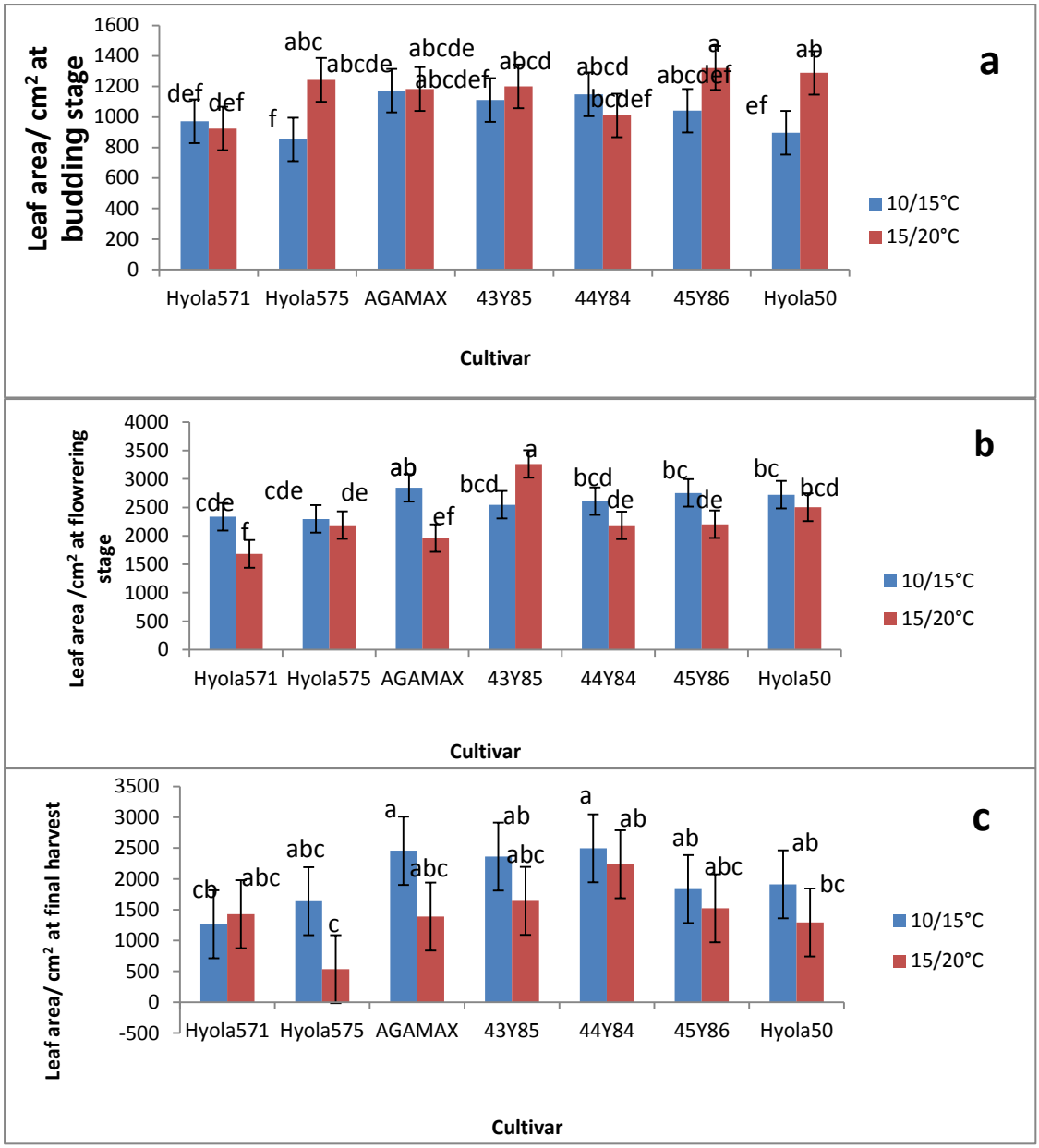

Figure 3 Leaf area plant^{-1} (cm2) of different canola cultivars , measured at (a)the beginning of budding (growth stage 3.1) (b) flowering and (c) during the final harvest at growth stage 5.4 in response to night/ day temperatures of 10/15^{0}C and 15/20^{0}C. *Values with the same alphabetical lettering do not differ significantly at P=0.05*

4.4 Dry mass

Above ground dry mass (g plant^{-1}) was measured at budding stage (growth stage 3.1), flowering stage (growth stage 4.1) and during the final harvesting when pods were physiological matured (growth stage 5.4). Above ground dry mass (g plant^{-1}) increased with time for all cultivars. The extent of DM accumulation was temperature-sensitive and cultivar dependent (Figure 4).

At budding stage (growth stage 3.1), a higher dry mass (g plant^{-1}) was generally, recorded for plants grown at the higher temperature regime of 15/20^{0}C, but differences were only significant for the cultivars Hyola 575, Hyola 50 and 45Y86.

At flowering, above ground dry mass was, with the exception of the early maturing cultivar 43Y85, significantly reduced when grown at the higher temperature regime of 15/20^{0}C. With the exception of Hyola 571, which produced significantly less dry mass than 43Y85, no differences were recorded between cultivars growing in the 15/20^{0}C glasshouse. In the cooler glasshouse (10/15^{0}C), the highest dry mass at flowering was produced by early and mid-early cultivars Hyola 571 and AGAMAX.

At final harvest (FH), no significant interaction between growing temperature regimes and cultivar was recorded, with dry mass of all cultivars reduced at the higher temperature regime of 15/20^{0}C (Figure 4). AGAMAX and 43Y85 recorded significantly higher dry mass than all other cultivars in the 15/20^{0}C, but only higher than Hyola 571 in the 10/15^{0}C glasshouse. In general, early and mid-early maturing types (Hyola 575,Hyola 571, AGAMAX and 43Y85) showed larger reductions in dry mass reductions of 41.31%, 34.69%, 39.65% and 40.65% respectively in the higher temperature glasshouse, while mid and mid to mid-early maturing types, 45Y86, Hyola 50 and 44Y84 showed reductions of 18.81%, 30.40% and 28.41%, respectively.

In general, crops at the 15/20^{o}C temperature regime, accumulated more above ground dry mass at the budding stage and more so for late maturing cultivars than at 10/15^{o}C temperature regime. It seems that the trait(s) for lateness enabled late maturing cultivars to produce more leaves by reducing the time between the appearances of successive leaves. Therefore; more leaves and leaf area recorded by late maturing cultivars at higher temperature regime during budding stage, as shown in figures 2 and 3, might be responsible for more above ground dry mass accumulated at budding stage. Canola crops have been reported to partition more dry mass to the leaves in the early growth stage than wheat, barley and sorghum (Rood et al., 1984, Deligios et al., 2013). In addition, Faraji et al., (2009) and Faraji (2014) showed significant positive correlations between leaf number before flowering and dry mass, as well as, final grain yield. Morrison et al. (1991) also reported that crops produced leaves at a slower rate when subjected to low temperature. For this reason, the higher dry mass accumulated at the 15/20^{o}C temperature regime compared to the 10/15^{o}C temperature regime, could be because leaves were produced at a faster rate.

Results from this study are in accordance with earlier studies (Qaderi et al. 2006, Gou, et al., 2010, Nordli et al., 2011), reporting an increase in dry matter production during earlier growth stages with higher temperatures, but a decrease in total dry mass production due to more rapid crop development and a shortened growth period.

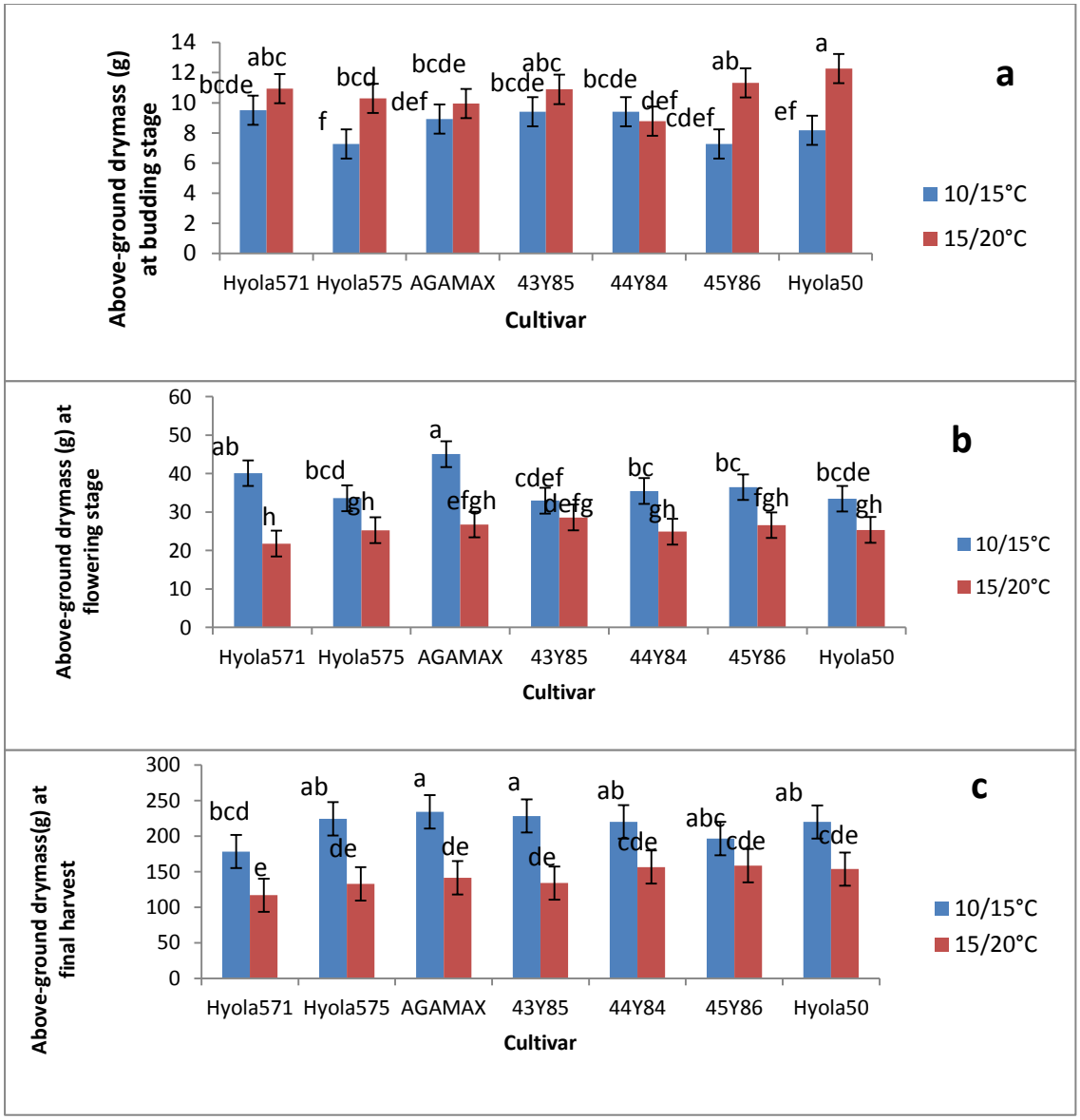

Figure 4 Dry mass (g plant^{-1}) of different canola cultivars, measured at (a)the beginning of budding (growth stage 3.1) (b) flowering and (c) during the final harvest at growth stage 5.4 in response to night/ day temperatures of 10/15^{0}C and 15/20^{0}C. *Values with same alphabetical lettering do not differ significantly at P=0.05*

4.5 Number of flower stems

The number of flower stems (plant^{-1}) was counted during the final sampling at growth stage 5.4 only.

Although all cultivars showed a decrease in the number of flower stems when grown at a lower temperature (10/15^{0}C) compared to 15/20^{0}C, differences were only significant for cultivar 44Y84 (Figure 5). With the exception of Hyola 575, cultivar 44Y84 produces significantly more flower stems compared to other cultivars at the lower temperature regime of 10/15^{0}C, but at the higher temperature regime (15/20^{0}C) no significant differences were recorded between cultivars.

The reduction in number of flower stems recorded in the higher temperature regime could be attributed to the fact that the higher temperature regime of 15/20^{0}C reduced the duration of different growth stages, so that plants had less time to develop flower stems. Similar results were reported by Kutcher et al. (2010) who found that high temperatures during vegetative growth reduced number of flowers produced per plant.

Except for the already mentioned difference between 44Y84 and other cultivars, at the lower temperature regime, the number of flower stem branches produced by different cultivars did not show any relationship with their maturity grouping as early and later maturing cultivars produced the same number of flower stems.

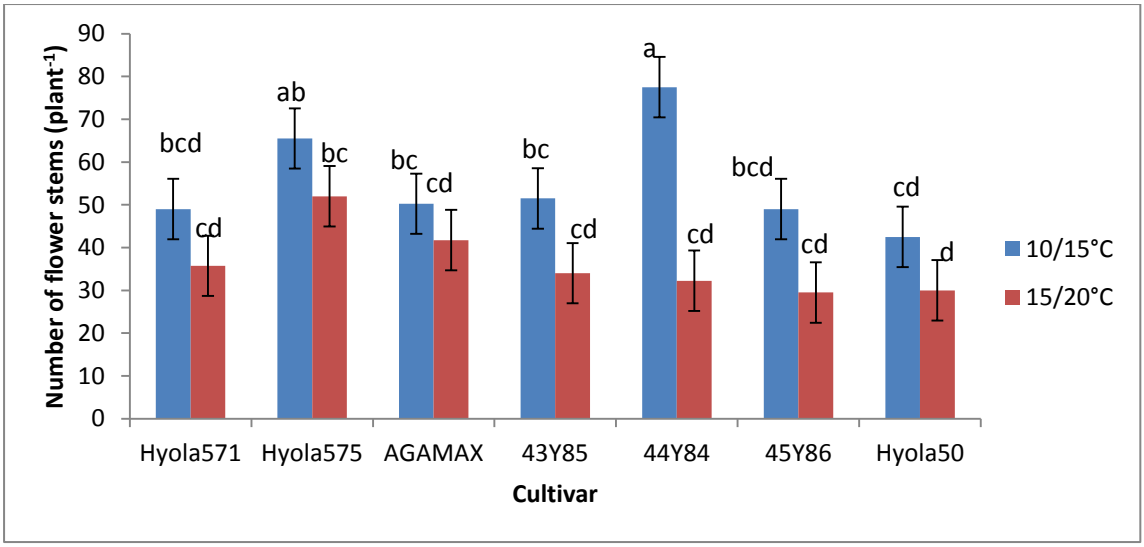

Figure 5 Flower stems (plant^{-1}) of different canola cultivars, measured during the final harvest at growth stage 5.4 in response to night/ day temperatures of 10/15^{0}C and 15/20^{0}C. *Values with the same alphabetical lettering do not differ significantly at P=0.05*

4.6 Number of pods

The number of pods (plant^{-1}) was counted during the final harvest at physiological maturity (growth stage 5.4) and ranged from 841 to 1483 pods (plant^{-1})

Cultivars differed with respect to the number of pods plant^{-1} when grown at different temperature regimes (Figure 6). With the exception of Hyola 50 and 44Y84, all cultivars produced significantly less pods (plant^{-1}) at the higher temperature regime (15/20^{0}C) compared to the 10/15^{0}C. However, differences between cultivars at both temperature regimes (10/15^{0}C and 15/20^{0}C) were not significant at ($p<0.05$). With exception of 45Y86, later maturing cultivars (44Y84 and Hyola 50) showed less reduction in the number of pods per plant in the higher temperature regime than early and mid-early maturing types.

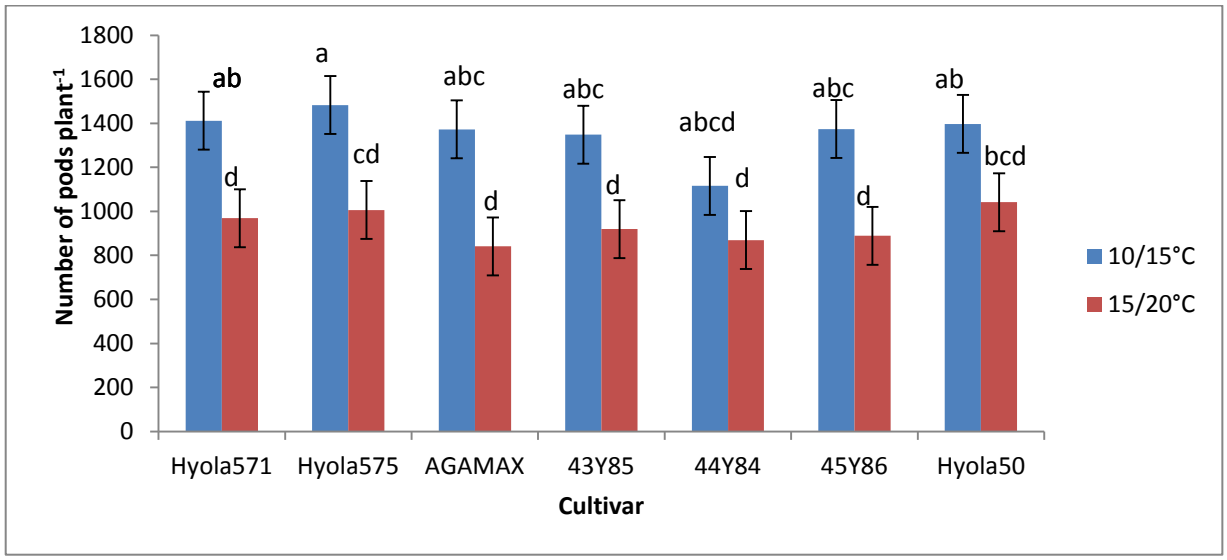

Figure 6 Effect of temperature on number of pods (plant^{-1}) of different canola cultivars, measured during the final harvest at growth stage 5.4 in response to night/ day temperatures of 10/15^{0}C and 15/20^{0}C. Values with the same alphabetical lettering do not differ significantly at P=0.05

4.7. Dry mass of pods

The dry mass of pods (plant^{-1}) was determined during the final harvest at the physiological matured growth stage 5.4.

Except 44Y84 and 43Y85, all cultivars showed a significant reduction in dry mass of pods plant^{-1} at the 15/20^{0}C temperature regime compared to the 10/15^{0}C temperature regime (Figure 7). Dry mass varied between about 80-116 g (plant^{-1}) at the lower day/night temperature of 10/15^{0}C and differences between cultivars were with the exception of, a significant higher pod dry mass in 45Y86 than 44Y84, No significant differences between cultivars were recorded at the 15/20^{0}C temperature regime and the pod dry mass (plant^{-1}) varied between about 58 and 72 g. Early maturing Hyola 575 and

Hyola 571 showed higher pods dry mass reductions than mid-maturing Hyola 50 with, an increase in temperature. In contrast to this, early maturing 43Y85 showed less response than mid-maturing 45Y86, indicating differences between cultivars from different breeding companies.

The reduced duration of crop growth stages, increased rate of respiratory breakdown of accumulated dry mass and accelerated leaf senescence due to the higher temperature might be the reason for the reduced pod dry mass at the 15/20^{0}C regime.

Kutcher et al. (2010) reported that increased mean temperature during vegetative development reduced the number of seeds and size of seed per flower and consequently resulted in seed yield reduction, the view also shared by findings of Morrison and Stewart (2002).

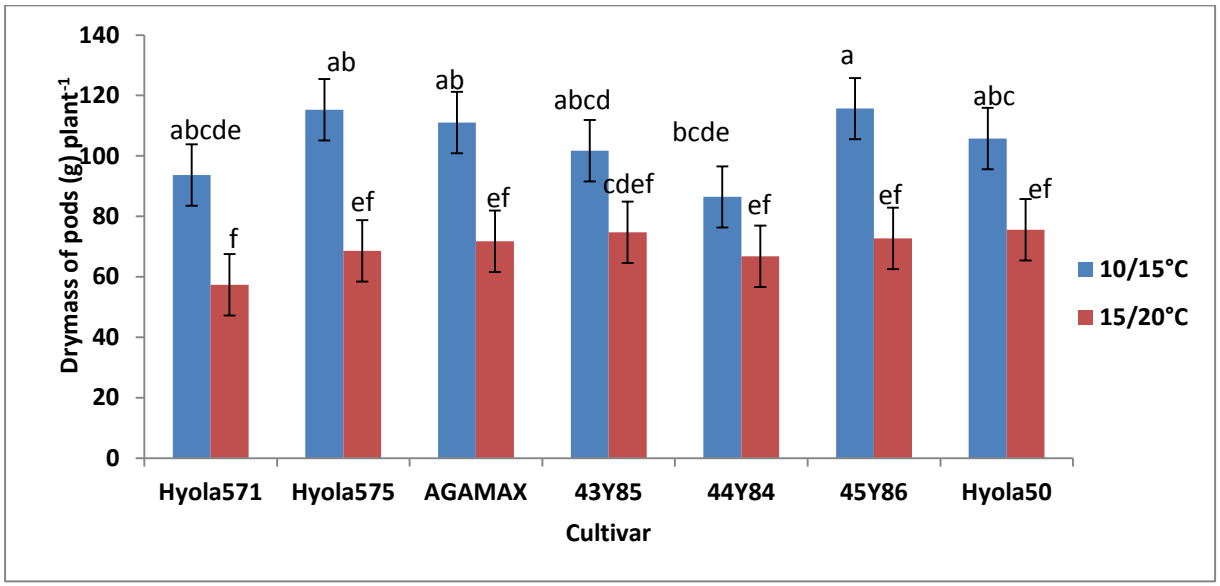

Figure 7 Pod dry mass plant^{-1} of different canola cultivars, measured during the final harvest at growth stage 5.4 in response to night/ day temperatures of 10/15^{0}C and 15/20^{0}C. Values with the same alphabetical lettering do not differ significantly at P=0.05

4.8 Effect of temperature on plant growth rate (PGR), relative growth rate (RGR) and net assimilation rate (NAR) of canola cultivars at budding, flowering and physiological maturity stages.

The PGR, RGR and NAR of different cultivars grown at temperatures of 10/15^{0}C and 15/20^{0}C were calculated using adapted formulas of Paine et al. (2012) for the periods: planting to budding (PGR only because plants do not have any leaf area at planting and dry mass of seeds were so small that RGR would be unrealistic), budding to flowering and flowering to physiological maturity, by using the mean number of days between the specific growth stages, plant dry mass (g) and leaf area (cm^2) (Table 1).

4.8.1 Plant growth rate (PGR).

Plant growth rate (PGR) increased progressively from planting to budding and from flowering to physiological maturity, at both temperature regimes (Table 1). On average a PGR of 0.2414 g (plant^{-1} day^{-1}) was recorded from planting to budding compared to 1.4452 g (plant^{-1} day^{-1}) and 2.0295 g (plant^{-1} day^{-1}), measured from budding to flowering and from flowering to physiological maturity. However, at each sampling stage, PGR differed as a result of both temperature and cultivars tested. From planting to budding, all cultivars showed a higher PGR at the 15/20^{o}C temperature regime compared to the 10/15^{o}C temperature regime, but from budding to flowering and flowering to physiological maturity a higher PGR was measured for all cultivars at the lower (10/15^{o}C) temperature regime compared to the 15/20^{o}C temperature regime. Cultivars also differed at both temperature regimes with respect to PGR. From planting to budding a PGR of 0.2752 g (plant^{-1} day^{-1}) was measured, on average, for the higher temperature regime of 15/20^{o}C compared to 0.2075 g (plant^{-1} day^{-1}) for the lower temperature regime (10/15^{o}C). At the 15/20^{o}C temperature regime, 45Y86 showed the highest PGR value, while Hyola 571 recorded the highest PGR value at the 10/15^{o}C temperature regime from planting to budding. From the budding to flowering stage, a higher PGR of 1.6124 g (plant^{-1} day^{-1}) were recorded on average by cultivars at the 10/15^{o}C temperature regime compared to 1.2780 g (plant^{-1} day^{-1}) on average at the 15/20^{o}C temperature regime. At the 10/15^{o}C temperature regime, AGAMAX recorded the highest PGR value, whereas at 15/20^{o}C temperature regime 43Y86 had the highest PGR value. Cultivars also showed a higher PGR at the lower temperature regime of 10/15^{o}c compared to higher temperature regime (15/20^{o}C) during the flowering to physiological maturity stage. At the 10/15^{o}C temperature regime cultivars grew at 2.2008 g (plant^{-1} day^{-1}) while at the 15/20^{o}C temperature cultivars grew at 1.8584 g (plant^{-1} day^{-1}) Cultivar, 43Y85 showed the highest PGR at 10/15^{o}C, whereas at 15/20^{o}C 44Y84 recorded the highest PGR from flowering to physiological maturity.

The increase in PGR from planting to physiological maturity indicated that PGR for all cultivars followed the normal growth rate curve, which usually increases as plant growth duration increase. Similar results have been reported for soybean, barley and maize (Garmash 2005, Liu et al. 2006, Thomas et al. 2010, Tsimba et al. 2013). Increased PGR from planting to budding at the 15/20^{o}C temperature regime and decrease from budding to flowering and flowering to physiological maturity suggest that increasing the mean night/day temperature, from 12.5^{o}C to 17.5^{o}C, increased PGR during the vegetative growth stage (planting to budding) by increasing the rate of leaf appearance and expansion, but as growth progress the increase in temperature decreased PGR by increasing the rate of leaf senescence and respiratory breakdown of photosynthates (Munier-Jolain et al. 2008, Tsimba et al. 20011, Tacarindua et al. 2012). Although differences in growth rate between cultivars were shown, it did not show any relationship with their maturity grouping.

4.8.2 Relative growth rate (RGR).

A higher relative growth rate (RGR) of 0.1528 g (g^{-1} day^{-1}) was shown, on average, from budding to flowering compared to a lower RGR of 0.0669 g (g^{-1} day^{-1}) from flowering to physiological maturity (Table 1). From budding to flowering, RGR was higher at the 10/15^{o}C temperature regime (0.1840 g (g^{-1} day^{-1}) than at the 15/20^{o}C temperature regime (0.1215 g (g^{-1} day^{-1}) , while from flowering to physiological maturity a higher RGR of 0.0727 g (g^{-1} day^{-1}) was recorded by cultivars at the 15/20^{o}C temperature regime compare to a PGR of 0.0610 g (g^{-1} day^{-1}) at the 10/15^{o}C temperature regime . AGAMAX showed the highest RGR at the 10/15^{o}C temperature regime, whereas at 15/20^{o}C temperature regime 44Y84 recorded the highest RGR from the budding to flowering stage. From flowering to physiological maturity 43Y85 showed the highest RGR at the 10/15^{o}C temperature, while AGAMAX showed the highest RGR at 15/20^{0}C.

The higher RGR observed from budding to flowering compared to that of flowering to physiological maturity could be attributed to the quantity of the dry mass at the beginning of the growth stage (DM_1). The RGR from budding to flowering was calculated by dividing PGR with dry mass at budding, while RGR from flowering to physiological maturity was calculated by dividing PGR with dry mass at flowering stage. The DM at the flowering stage was higher than DM at the budding stage, therefore as (DM1) increases RGR within any range of growth stages decreases. The same applies for differences between temperature regimes, dry mass at budding stage were higher at 15/20^{o}C temperature regime, so there was lower RGR from budding to flowering stage and vice-visa, while at flowering stage dry mass were higher at the10/15^{o}C temperature regime and lower RGR were observed from flowering to physiological maturity and vice-visa. Similar trends of RGR have been observed for wheat, soybean and maize (Victor et al. 2006, Federick et al. 2013, Tacarindua etal. 2013, Tsimba et al. 2013) and therefore show that the efficacy of crops to accumulate dry mass decreases towards the end of the growing season . Differences between cultivars did not show any relationship with maturity grouping.

4.8.3 Net assimilation rate (NAR).

A higher NAR of 0.00136 g (cm^{-2} day^{-1}) was recorded by cultivars at both temperature regimes from budding to flowering when compared to the 0.00083 g (cm^{-2} day^{-1}) from flowering to physiological maturity. From budding to flowering cultivars recorded higher NAR of 0.00161 g (cm^{-2} day^{-1}) at the 10/15^{o}C temperature regime compared to the 0.00111 g (cm^{-2} day^{-1}) at the 15/20^{o}C temperature regime. From flowering to physiological maturity there was no difference between NAR at different temperature regimes. Cultivars of the same maturity groups did not show similar NAR values at different sampling stage or temperature regimes.

At the 10/15^{o}C temperature regime Hyola571 recorded the highest NAR from budding to flowering, while 43Y85 showed the highest NAR at 15/20^{o}C. From flowering to

physiological maturity there were no difference between temperature regimes, but cultivars did differ. At the 10/15^{o}C temperature regime Hyola 575 showed the highest NAR, whereas all cultivars, with the exception of 43Y85, showed NAR values of 0008-0009 g (cm^{-2} day^{-1}) at the 15/20^{o}C temperature regime.

The higher NAR recorded from budding to flowering stage than from flowering to physiological maturity can be attributed to lower leaf area at budding stage (LA1), which was used as the divisor of the PGR from budding to flowering and higher leaf area at flowering (LA1) which was use as divisor of PGR from flowering to physiological maturity. These results agreed with findings of Gaetan et al. (2008) and John and Kim (2014) whom also showed that NAR and therefore photosynthetic efficiency of plants decrease towards the end of the growing season.

Table 1 Effect of temperature on plant growth rate (PGR) g (plant^{-1}day^{-1}), relative growth rate of plants (RGR) g (g^{-1} day^{-1}) and net assimilation rate of plants (NAR) g (cm^{-2}day^{-1}) of the different canola cultivars determined for the periods: Planting to budding; Budding to flowering and from flowering to physiological maturity.

		Planting to budding	Budding to flowering			Flowering to physiological maturity		
Temp	**Cultivar**	**PGR**	**PGR**	**RGR**	**NAR**	**PGR**	**RGR**	**NAR**
10/15^{0}C	Hyola571	0.2315	2.04	0.215	0.0021	1.7377	0.0433	0.0007
	Hyola575	0.1773	1.645	0.2269	0.0019	2.414	0.0719	0.0011
	AGAMAX	0.2178	2.1241	0.2379	0.0018	2.3058	0.0512	0.0008
	43Y85	0.2176	1.3847	0.1472	0.0013	2.5697	0.078	0.001
	44Y84	0.2136	1.303	0.1385	0.0013	2.1754	0.0613	0.0008
	45Y86	0.209	1.6135	0.1785	0.0016	1.8589	0.051	0.0007
	Hyola50	0.1857	1.1763	0.144	0.0013	2.3432	0.07	0.0007
10/15^{o}Cmean		**0.2075**	**1.6124**	**0.184**	**0.00161**	**2.2008**	**0.061**	**0.00083**
15/20^{0}C	Hyola571	0.2957	1.086	0.0993	0.0012	1.5571	0.0714	0.0009
	Hyola575	0.2765	1.0736	0.105	0.0009	1.886	0.0747	0.0008
	AGAMAX	0.2692	1.3177	0.1323	0.0011	1.9666	0.0735	0.0009
	43Y85	0.2656	1.6456	0.1511	0.0014	1.8259	0.0639	0.0006
	44Y84	0.2144	1.3425	0.1527	0.0013	1.9567	0.0786	0.0009
	45Y86	0.3062	1.1723	0.1035	0.009	1.898	0.0714	0.0009
	Hyola50	0.299	1.308	0.1067	0.001	1.9185	0.0757	0.0008
15/20^{o}Cmean		**0.2752**	**1.278**	**0.1215**	**0.00111**	**1.8584**	**0.0727**	**0.00083**
GSmean		**0.2414**	**1.4452**	**0.1528**	**0.00136**	**2.0295**	**0.0669**	**0.00083**

GSmean (growth stage mean)

Conclusions

The study demonstrated that an increase in night/day temperature from 10/15^{0}C to 15/20^{0}C resulted in an increase in plant height, leaf number at budding stage, leaf area at budding, plant growth rate from planting to budding stage, but reduced plant growth

rate from budding to physiological maturity, net assimilation rate from the budding to flowering stage, leaf area at flowering and physiological maturity, as well as the number of flower stems, number of pods (plant^{-1}), above ground dry mass at flowering and physiological maturity stages and pod dry mass at the physiological maturity stage by 22.24% to 40.35%.

It also showed that, on average, later maturing (mid-maturing) cultivars produced more leaves, leaf area at the budding, flowering and physiological maturity stages, as well as above ground dry mass at budding stage, compared to early maturing cultivars. However, they produce less flower stems and pods (plant^{-1}). At physiological maturity, early maturing cultivars (Hyola 575 and Hyola 571) showed the highest reduction in pods dry mass of 40.35% and 38.28%, respectively, with an increase in temperature to 15/20^{0}C. Surprisingly, the early maturing 43Y85 shared most of morphological characteristics of later maturing (mid- maturing) types instead of those of early and mid-early types, indicating that the response of different cultivars to an increase in temperature might to a large degree be related to their genetics (breeding company) and not to their maturity grouping.

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CHAPTER 5

Effect of temperature on phenological responses of seven canola cultivars

Results and discussion

5.1 Germination (Planting to seedling emergence)

Number of days after planting (NDAP), growing degree days (GDD) (^{0}Cd) and photothermal units (PTU) (^{0}Cdhr) required from planting date to seedling emergence of the different cultivars in response to the two temperature regimes (10/15^{0}C and 15/20^{0}C) are shown in Figure 8.

The number of days needed from planting for seedlings to emerge were for all cultivars, significant less ($p<0.05$) at the higher temperature regime (15/20^{0}C) than at the lower temperature regime of 10/15^{0}C (Figure 8a). At the lower temperature regime of 10/15^{0}C, cultivars needed about six days for seedlings to emerge, but cultivar 43Y85 needed significantly more days than all other cultivars except 44Y84 and Hyola 50. At the higher temperature regime of 15/20^{0}C, seedlings emerged after about five days and no significant differences were recorded between cultivars. On average, the increase in temperature from 10/15^{0}C to 15/20^{0}C temperature regime reduced the number of days from planting to seedling emergence by 1.21 days. Number of days needed from planting to emergence did not show any relationship with the maturity grouping of cultivars.

In contrast to the number of days, significantly more GDD were needed for all cultivars from planting to seedling emergence when exposed to the higher temperature regime of 15/20^{0}C compared to the 10/15^{0}C temperature regime (Figure 8b). In the 15/20^{0}C glasshouse all cultivars needed about 85 GDD for seedlings to emerge and no significant differences between cultivars were recorded. In the 10/15^{0}C glasshouse, about 76 GDD were needed and no differences between cultivars were again recorded. No clear trend of cultivar response with regard to maturity types was noticed.

Because PTU were calculated by multiplying GDD with hours of day length and all cultivars were grown at the same day lengths at both temperature regimes, PTU requirement for seedlings to emerge were also significantly higher for all cultivars at the higher temperature regime (15/20^{0}C), than at the lower temperature regime of 10/15 (Figure 8c). No significant differences between cultivars were recorded at any of the two temperature regimes. On average about 1 000 PTU were needed for seedlings to emerge at the 10/15^{0}C temperature regime compare to about 1 150 at the 15/20^{0}C temperature regime. No clear trend with regard to PTU requirements for different maturity groups was shown.

Except for number of days at the lower temperature regime, no significant differences between cultivars were shown with regard to number of days, GDD or PTU requirements for seedlings to emerge.

Qi, et al., (1999) also found no differences between 12 Mucuna cultivars with regard to number of days from sowing to seedling emergence.

However, temperature did effect the number of days for seed to germination and this was expected, since seed germination is a biochemical process that involve water absorption, activation and synthesis of enzymes, oxidation of stored food, transport of oxidates within the embryo and initiation of embryonic growth (Mills,1993). The higher temperature regime of 15/20^{0}C, most probably increased the rate of these biochemical processes and thereby reduced the time required for the seedlings to emerge as shown by Vigil et al., (1997). The results of this study are also in agreement with the report of Mendham and Salisbury (1995), who concluded that increased temperature reduced the duration of all growth stages of canola.

On average 6 - 6.5 and 4.8 - 5.0 days were needed for seedlings to emerge at the temperature regimes of 15/20^{0}C, and 10/15^{0}C respectively in this study, which are similar to the results obtained by Robertson (2002) on a large number of localities in NSW, Australia, but differ from the 8-11 days needed under field conditions at two localities in Central Western Australia (Hertel 2012). It is however very difficult to compare germination data from field studies with that of pot trials in glasshouse studies, because soil moisture content may have a large effect under field conditions.

GDD is a product of the number of days and mean temperature (base temperature = 0^{0}C). For this reason, even the reduced number of days from planting to seedling emergence at the 15/20^{0}C glasshouse, resulted in a higher number of GDD (83.34-87.82 degree-days) compared to 75.04-81.50 degree-days at the 10/15^{0}C glasshouse temperature. The difference in number days between the two temperature regimes was not big enough to compensate for the difference in temperature. Vigil et al. (1997) also reported that *B napus* requires 75-120 degree-days from planting to seedling emergence seed germination. Similarly Robertson (2002) reported a mean GDD requirement of 115 degree-days for 12 canola cultivars tested.

Because Photothermal unit (PTU) was calculated as GDD x daylength and day length was the same for both temperature regimes, PTU showed the same trend as GDD in this study, but as *Brassica* spp generally did not show any photosensitivity during the germination stage (Qaderi and Reid 2005) no effect was expected .

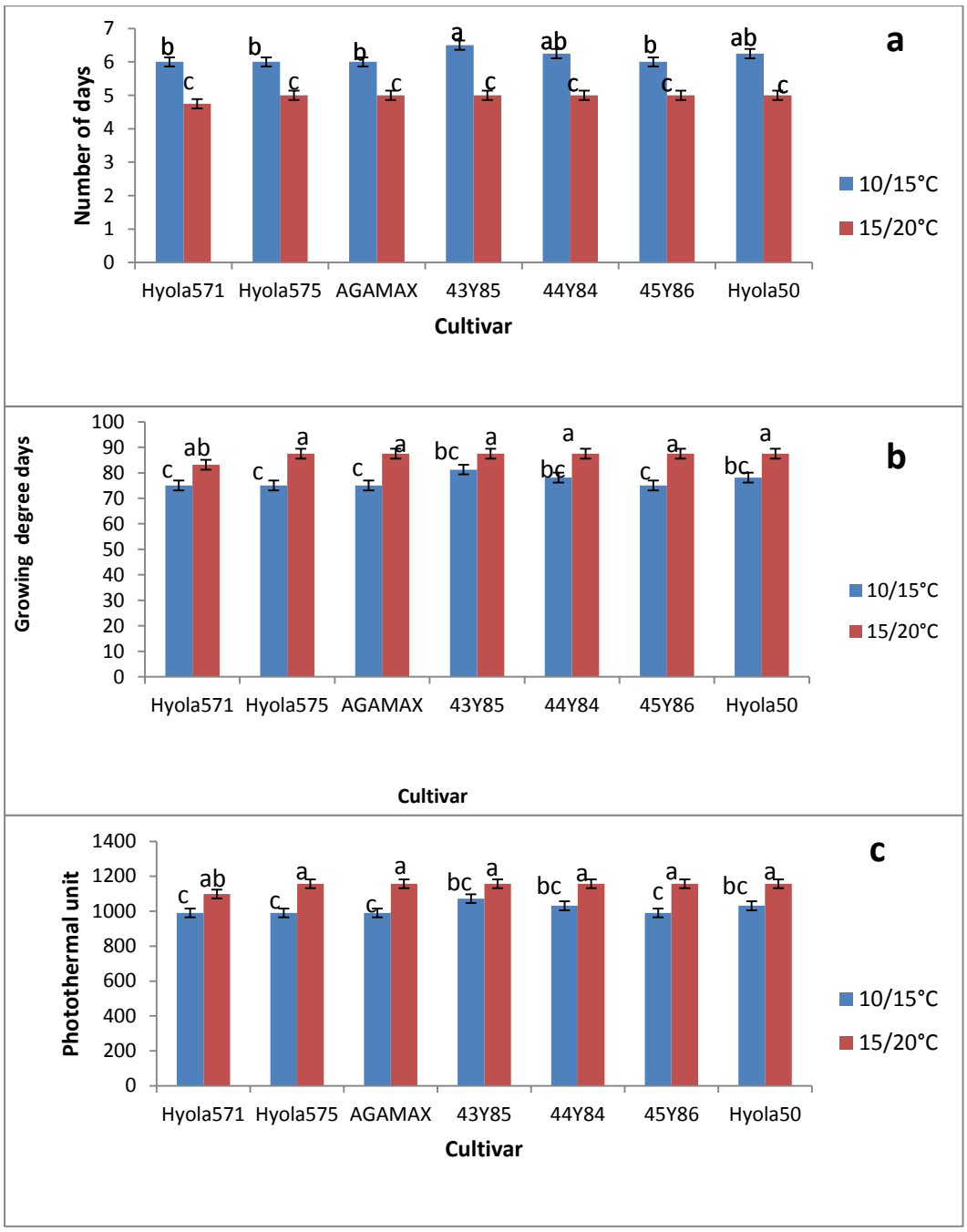

Figure 8 Effect of temperature on a) the number days, b) growing degree days (degree-days) and c) photothermal units (degree-hour-days) required from planting till seedling emergence of different cultivars. Values/ bars with the same alphabetical lettering do not differ significantly at P=0.05

5.2 Vegetative growth (rate of leaf appearance)

Vegetative growth spans from appearance of the first true leaf (2.1) to budding stage (3.1) which is the end of the vegetative growth stage and beginning of reproductive growth. Number of days, GDD (degree days) and PTU (degree-hour days) required by

different cultivars from planting to reach growth stage 2.1 (first true leaf) in response to night/day temperatures of 10/15^{0}C and 15/20^{0}C are shown in Figure 9.

In general, cultivars required significantly ($P<0.05$) more days from planting to first true leaf appearance at the 10/15^{0}C temperature regime than at the 15/20^{0}C temperature regime (Figure 9a). At temperatures of 10/15^{0}C all cultivars required, on average, 12.65 days to the first true leaf to appear, with Hyola 571 requiring significantly more days than other cultivars and 43Y85 significantly less than 44Y84 and 45Y86. At the 15/20^{0}C temperature regime, cultivars required, on average, 7.6 days for the first true leaf to appear and no significant differences between cultivars were recorded. The increase in temperature from 10/15^{0}C to 15/20^{0}C reduced the number of days for the first true leaf to appear by 5.05 days. No clear trend with regard to number of days to first true leaf appearance for different maturity groups was shown.

Similar to the number of days, significantly more GDD were required at the 10/15^{0}C temperature regime compared to 15/20^{0}C temperature regime (Figure 9b). At the 10/15^{0}C temperature regime cultivars required on average 151.34 degree-days to first true leaf appearance, whereas 133.13 degree-days were required at the 15/20^{0}C temperature regime. At the 10/15^{0}C temperature regime Hyola 575, Hyola 571, Hyola 50 and AGAMAX were not significantly different to each other, but needed significantly more GDD than 43Y85, 44Y84 and 45Y86. Similarly, at 15/20^{0}C, AGAMAX required significantly more GDD than 43Y85, 44Y84 and 45Y86, but not significantly more than Hyola 575, Hyola 50 and Hyola 571.

Cultivars requirement for PTU to first true leaf appearance, at both temperature regimes, followed the same trend as GDD. At the lower temperature of 10/15^{0}C all cultivars, with exception of 43Y85, required significantly more PTU to first true leaf appearance than at the 15/20^{0}C temperature regime. On average 1978.16 degree-hour-days were required at 10/15^{0}C, compared to about 1756.43 degree-hour-days required at the higher temperature regime of 15/20^{0}C. At the lower temperature regime (10/15^{0}C) PTU requirements for Hyola 50, Hyola 575, Hyola 571 and AGAMAX were not significantly different, but needed significantly more PTU than 43Y85, 44Y84 and 45Y86. Similarly, at the 15/20^{0}C temperature regime, Hyola 50, Hyola 575, AGAMAX and Hyola 571 required significantly more PTU from planting to first true leaf appearance than 43Y85, 44Y84 and 45Y86.

Increase in the night/day temperature from 10/15^{0}C to 15/20^{0}C reduced number of days, GDD and PTU to first true leaf appearance. Cultivar responses to these temperature regimes, with regard to number of days, GDD and PTU, did not correlate with their maturity grouping, but all cultivars from the breeding company, DuPont Pioneer® (43Y85, 44Y84 and 45Y86) required less GDD and PTU than cultivars from other breeding companies tested.

The significantly higher number of days to first true appearance on Hyola 571 at the 10/15^{0}C temperature regime might have occurred by chance and not as a result of intrinsic trait(s) for earliness, since other cultivars of the same maturity group did not show a similar trend. Thus, it can be concluded that, cultivars did not differ within each temperature regime with respect to number of days needed from planting to first true leaf appearances. However, since first true leaf appearance marked the beginning of vegetative growth stage and not the end, it is possible that as vegetative growth progresses, there might be differences as due to differences in duration between successive leave appearances for each cultivar. Such differences will however be shown when days to budding are presented. Kasa and Kondra (1984) as well as Nanda et al. (1995) reported that B *compestris* had a faster leaf emergence rate than B. *napus* and *B. carinata* during all growth periods, but also did not show differences between species.

Temperature has a significant effect on the number of days to first true leaf appearance and this could be attributed to a higher heat units as a result of higher mean temperature. The higher temperature (heat units) increase the growth rate of crops and therefore might reduce the duration of vegetative growth phase in the 15/20^{0}C temperature regime. Daily mean temperatures of 22^{0}C to 25^{0}C have been reported to increase leave appearance rate and reduced the duration of vegetative growth phase of summer rape (Morrison et al. 1992). Similarly, Qaderi et al. (2006) reported that a daily mean temperature of 26^{0}C increased leaf growth rate of canola cultivar 42H72 when compared to daily mean temperatures of 20^{0}C. Increased rate of leaf production and reduction in duration of vegetative growth phase by increased temperature within the range of optimum requirement have also been reported for wheat, barley and soybean (Hofstra et al. 1977, Gallagher 1979). Nanda et al. (1995) reported similar results and showed that for each 1^{0}C reduction in temperature, there was an equivalent delay of 1.35 days for plants to reach the in first true leaf stage.

Since GDD was calculated by number of days x mean daily temperatures, which were fixed at 12.5 and 17.5^{0}C for our lower and higher temperature regimes respectively, the significant reduction in GDD at the 15/20^{0}C temperature regime was because of reduced number of days required to this growth stage at the higher temperature regime, this has also been reported for chickpea by Soltani et al., (2006). As temperature increases the phyllochron (thermal time between emergences of successive leaves measured in degree-days) decreases.

Photothermal units (PTU) was calculated by GDD x daylength and daylength was the same for both temperature regimes (about 12:53hours at this stage) trends were similar to that of GDD.

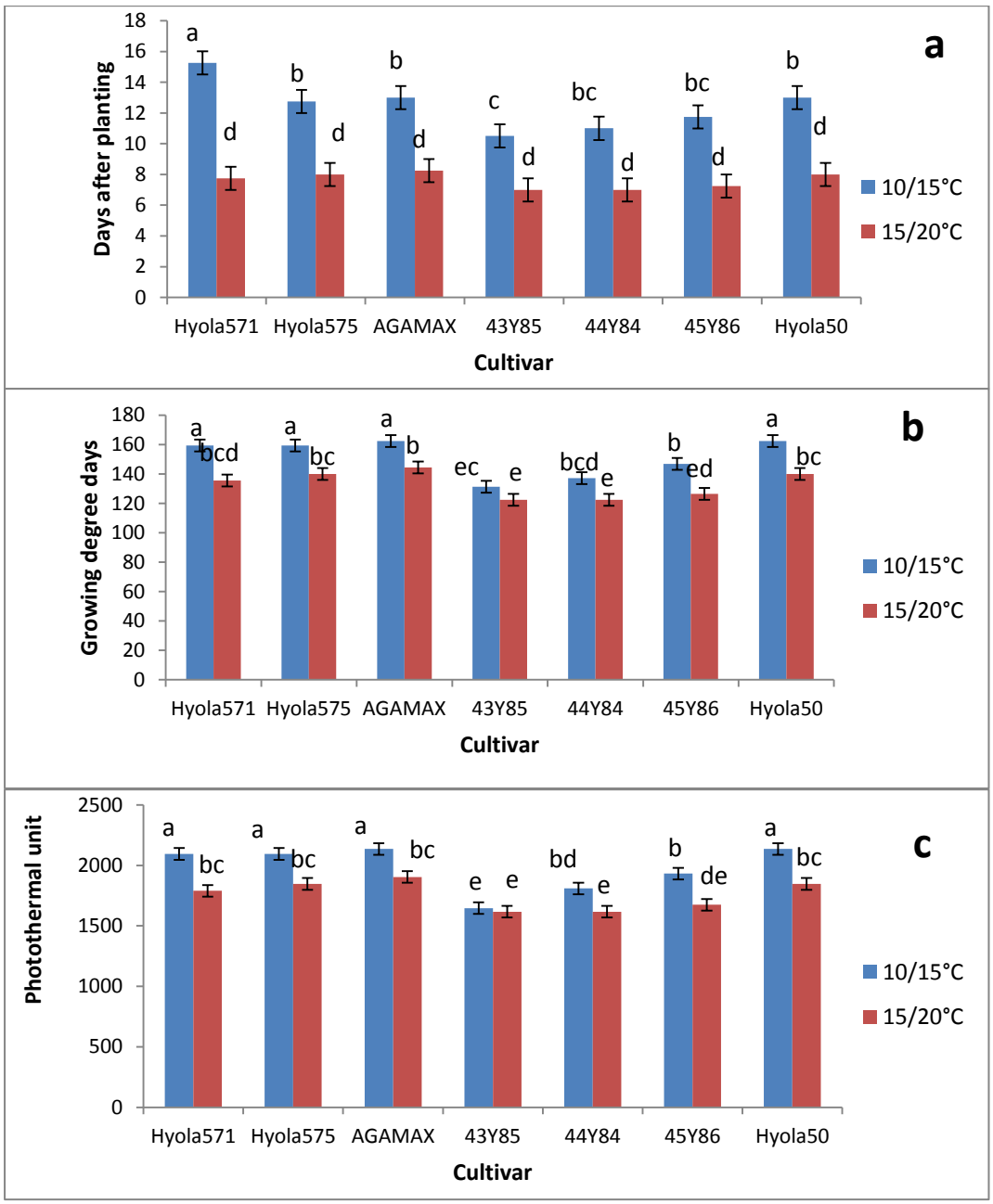

Figure 9 Effect of temperature on a) the number days, b) growing degree days (degree-days) and c) photothermal units (degree-hour-days) required from planting till first true leaf appearance of different cultivars. Values/ bars with the same alphabetical lettering do not differ significantly at P=0.05

5.3 Reproductive growth stages

Reproductive growth stages start at budding and continue through flowering and pods filling, to physiological maturity stage. Although each stage consist of several sub-stages, calculations were done for budding (3.1), flowering (4.1), seed ripening (5.1) and physiological maturity (5.4) stages only.

5.3.1 Budding

Budding stage is characterized by appearance of flower buds in the terminal region and stem elongation (Slauenwhite and Qaderi. 2013). Number of days, GDD(degree-days) and PTU(degree-hour-days) required by the seven cultivars from planting date to budding stage in response to day/night temperature regimes of 10/15^{0}C and 15/20^{0}C, is shown in Figure 10.

At the lower temperature regime of 10/15^{0}C, cultivars required significantly more days from planting to the budding stage than at the higher temperature regime of 15/20^{0}C (Figure 10). At the 10/15^{0}C temperature regime cultivars required about 42.5 days from planting to budding and Hyola 50, 44Y84, 43Y85 and 45Y86, were not significantly different to each other, but required significantly more days from planting to budding than Hyola 571, Hyola 575 and AGAMAX. At the 15/20^{0}C temperature regime cultivars required about 38.71days from planting to budding and Hyola 50, 44Y84 and 43Y85 did not differ significantly, but required more days than Hyloa 571, Hyloa 575, AGAMAX and 45Y86.

In contrast to number of days, cultivars required significantly more GDD at higher night/day temperature regime of 15/20^{0}C than at the lower night/day temperature regime of 10/15^{0}C (Figure 10b). On average 677.5 degree-days were required by cultivars at the 15/20^{0}C temperature regime. Similar to number of days Hyola 50, 44Y84 and 43Y85 were not significantly different to each other but required significantly more GDD than Hyola 571, Hyola 575, AGAMAX and 45Y86. At the 10/15^{0}C temperature regime cultivars required 529.91 degree-days on average from planting to budding and Hyola 50, 44Y84 were not significantly different to each other or 43Y85, but required significant more GDD than Hyola571, Hyola575, AGAMAX and 45Y86.

Cultivars PTU requirements from planting to budding stage differ between the temperature regimes (Figure 10c). At the higher temperature regime of 15/20^{0}C cultivars required significantly more PTU than at the lower temperature regime of 10/15^{0}C. On average 8398.59 degree-hour-days were required at the 15/20^{0}C temperature regime with no significant differences between cultivars. At the lower temperature regime (10/15^{0}C) cultivars required on average 4737.63 degree-hour-days from planting to budding stage with significant differences between cultivars. Hyola50, 44Y84 and 45Y86 were not significantly different to each other or Hyola 571 and AGAMAX, but required significant more PTU than Hyola 575 and 43Y85.

Increase in night/day temperatures from 10/15^{0}C to 15/20^0 resulted in reduced number of days, increased GDD and PTU from planting to budding stage. Except for PTU at the 15/20^{0}C, cultivars showed significant differences with regard to number of days, GDD or PTU required from planting to budding stage. In general, later maturing cultivars such as Hyola 50, 45Y86 and 44Y85 tend to need more days and GDD, but not PTU to reach the budding stage when compared to Hyola 575, Hyola 571 and AGAMAX suggesting that the later maturing cultivars have a longer vegetative period. However cultivar 43Y85 which is classified as an early maturing cultivar responded in a similar way than later maturing cultivars. Angadi et al. (2000) similarly observed different responses for three Brassica species to temperatures of 20/15^{0}C, 28/18^{0}C and 35/15^{0}C at the onset of the reproductive growth phase. Results agreed with the findings of Hartel (2012) who reported that canola grown under mean temperatures of 10.2^{0}C and 13.2^{0}C required 75 and 62 days from sowing to stem elongation (budding) stage and subsequently accumulated 760 degree-days and 747 degree-days respectively.

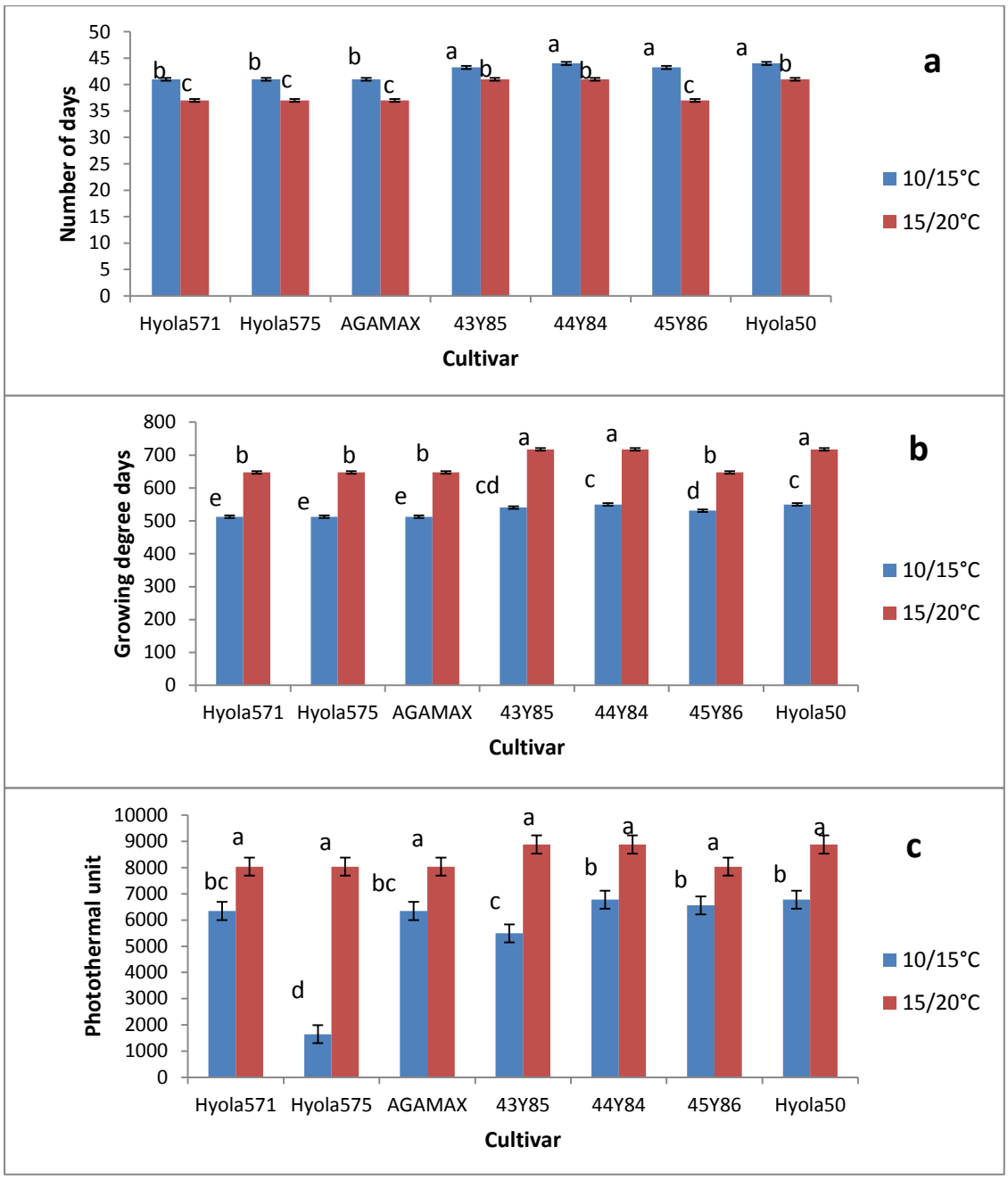

Figure 10 Effect of temperature on a) the number days, b) growing degree days (degree-day) and c) photothermal units (degree-hour-days) required from planting till first true s leaf appearance of different cultivars. Values/ bars with the same alphabetical lettering do not differ significantly at P=0.05

5.3.2 Flowering

Number of days, GDD and PTU required for all cultivars from planting to flowering (growth stage 4.1) in response to night/day temperature regimes of 10/15^{0}C and 15/20^{0}C are shown in Figure 11.

At the 10/15^{0}C temperature regime cultivars required significantly more days from planting to flowering than at the 15/20^{0}C temperature regime (Figure 11a). At lower temperature regime cultivars required 60.32 days on average to reach the flowering stage. Significant differences were noticed between cultivars. Hyola 50 did not require significantly more days than 44Y84, but required significantly more days to flower than other cultivars. At higher temperature regime, cultivars on average required 50 days, an average from planting to flowering (growth stage 4.1) and although 44Y84 did not need more days than Hyola 50, 43Y85 and 45Y86, it needed significantly more than Hyola 571, Hyola 575 and AGAMAX.

The GDD requirement from planting to flowering increased significantly with an increase in night/day temperature from 10/15^{0}C to 15/20^{0}C (Figure 11b). On average, 871.25 degree-days were required at 15/20^{0}C compared to 754.02 degree-days at 10/15^{0}C. No significant differences were recorded at 15/20^{0}C between cultivars 44Y84, 43Y85, Hyola50 and 45Y86, but these cultivars required significantly more GDD from planting to flowering than Hyola 571, Hyola 575 and AGAMAX. At 10/15^{0}C, Hyola 50 required, with the exception of 45Y84, significant more GDD from planting to flowering than other cultivars tested..

Similarly, PTU requirement from planting to flowering also increased with increase in night/day temperature from 10/15^{0}C to 15/20^{0}C (Figure 11c). At higher temperatures cultivars required on average 10651 degree-hour-days compared to 9096 degree-hour-days at 10/15^{0}C. Cultivars, Hyola 50, 45Y86, 44Y84 and 43Y85, required significantly more PTU from planting to flowering than other cultivars at the higher temperature regime. At 10/15^{0}C, Hyola 571 required the lowest number of PTU and Hyola 50 the highest number of PTU to reach flowering stage. Cultivars, Hyola 50 and 44Y84 required significantly more PTU to reach flowering stage than other cultivars tested, while 43Y85 required more PTU to reach flowering than Hyola 571, Hyola 575 and AGAMAX.

Higher night/day temperature of 15/20^{0}C reduced number of days but increased GDD and PTU needed to develop from planting to flowering when compared to a lower night/day temperature of 10/15^{0}C. Cultivars responded differently at each temperature regime with respect to number of days, GDD and PTU needed to reach flowering stage.

The rate of biochemical reactions, including those involved in mechanisms of crops to flower are generally faster as temperature increases. Therefore, the reduction in number of days to flowering of 10.38 days, on average at the higher temperature regime compared to the lower temperature regime could be as a result of this catalytic acceleration of biochemical processes involved as also shown by quite a number of previous studies (Fitter and Fitter, 2002, Hepper 2003, Kaesha 2009). Robertson (2002) also reported that increased temperature between 12 and 20^0C reduced number of days to flowering in 21 canola cultivars. Similar results were also reported by Tacarindua et al. (2013) for soybeans grown in a temperature gradient chamber.

On average, later maturing cultivars such as Hyola 50, 45Y86 and 44Y84 required more days, GDD and PTU to reach flowering stage than early maturing Hyola 471, Hyola 575 and AGAMAX. However, 43Y85 which is described as an early maturing cultivar, but from a different breeding company, responded similar to later maturing cultivar of the same breeding company. Robertson et al. (2002) reported that an early maturing canola type such as Monty required in the range of 44-109 days to flowering, while mid maturing cultivars such as Hyola 42 required between 44-118 days and late maturing Pinnacle required between 47-124 days to flower, depending on day length and soil fertility conditions. Similarly Slauenwhite and Qaderi (2013) reported that there were significant differences between four canola cultivars with respect to number of days to flowering and GDD accumulated at flowering.

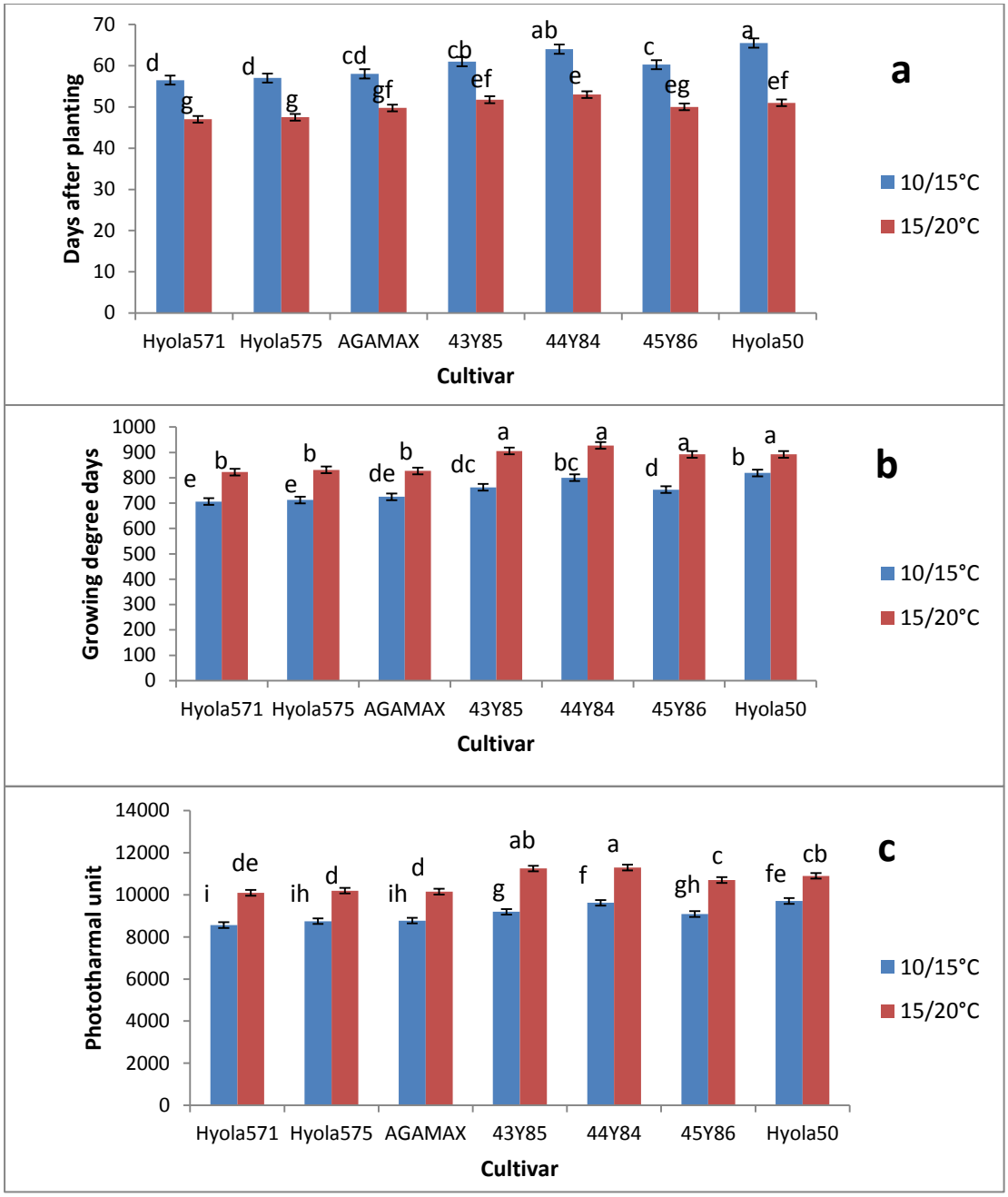

Figure 11 Effect of temperature on a) the number days, b) growing degree days (degree-days) and c) photothermal units (degree-hour-days) required from planting till first flower opening on cultivars. Values/ bars with the same alphabetical lettering do not differ significantly at P=0.05

5.3.3 Seed ripening

Number of days, GDD and PTU required by different cultivars, grown at either 10/15^{0}C, or 15/20^{0}C to reach the seed ripening stage (growth stage 5.1) are shown in Figure 12.

Number of days from planting to the seed ripening stage was significantly more when grown at 10/15^{0}C compared to 15/20^{0}C (Figure 12a). At the 10/15^{0}C temperature regime, 102.42 days were required on average, to reach the seed ripening stage. Significant differences between cultivars were recorded with Hyola 50, 44Y84 and 43Y85 requiring more days than 45Y86, AGAMAX, Hyola 571 and Hyola 575. When grown at a night/day temperature of 15/20^{0}C , cultivars required on average 77.21 days from planting to reach seed ripening stage, with 44Y84 and 45Y86 requiring significantly more than other cultivars.

With the exception of 43Y85 and Hyola 50, all cultivars required significantly more GDD from planting to seed ripening at the 15/20^{0}C temperature regime that at the 10/15^{0}C temperature regime (Figure 12b). On average, 1347.64 degree-days were required from planting to seed ripening at the 15/20^{0}C temperature regime, with 44Y84 and 45Y86 requiring significantly more GDD than other cultivars. At the 10/15^{0}C temperature regime, cultivars required on average 1277.23 degree-days to reach the seed ripening stage with the exception of 43Y85 and 44Y84, Hyola 50 required significantly more GDD than other cultivars.

Similarly, with exception of 43Y85, PTU requirements for cultivars to reach the seed ripening stage were significantly more at 15/20^{0}C than at 10/15^{0}C (Figure 12c). On average 15347.7 degree-hour-days were required from planting to seed ripening at the 15/20^{0}C temperature regime. Cultivar 44Y84, required significantly more PTU than other cultivars. At the 10/15^{0}C temperature regime, 14108.23 degree-hour-days were required on average, but Hyola 50, 44Y84 and 43Y85 required significantly more PTU than other cultivars.

The increase in night/day temperatures from 10/15^{0}C to 15/20^{0}C reduced the number of days and with the exception of 43Y85 and Hyola 50, increased GDD and PTU from planting to seed ripening. Although significant differences were recorded between cultivars and their responses to increasing night/day temperature, responses did not show a clear relationship with maturity grouping.

Hartel (2012) also reported that the responses of crops to mean temperatures of 10.2^{0}C and 13.2^{0}C after the end of flowering were increased at a greater rate when compared to before flowering.

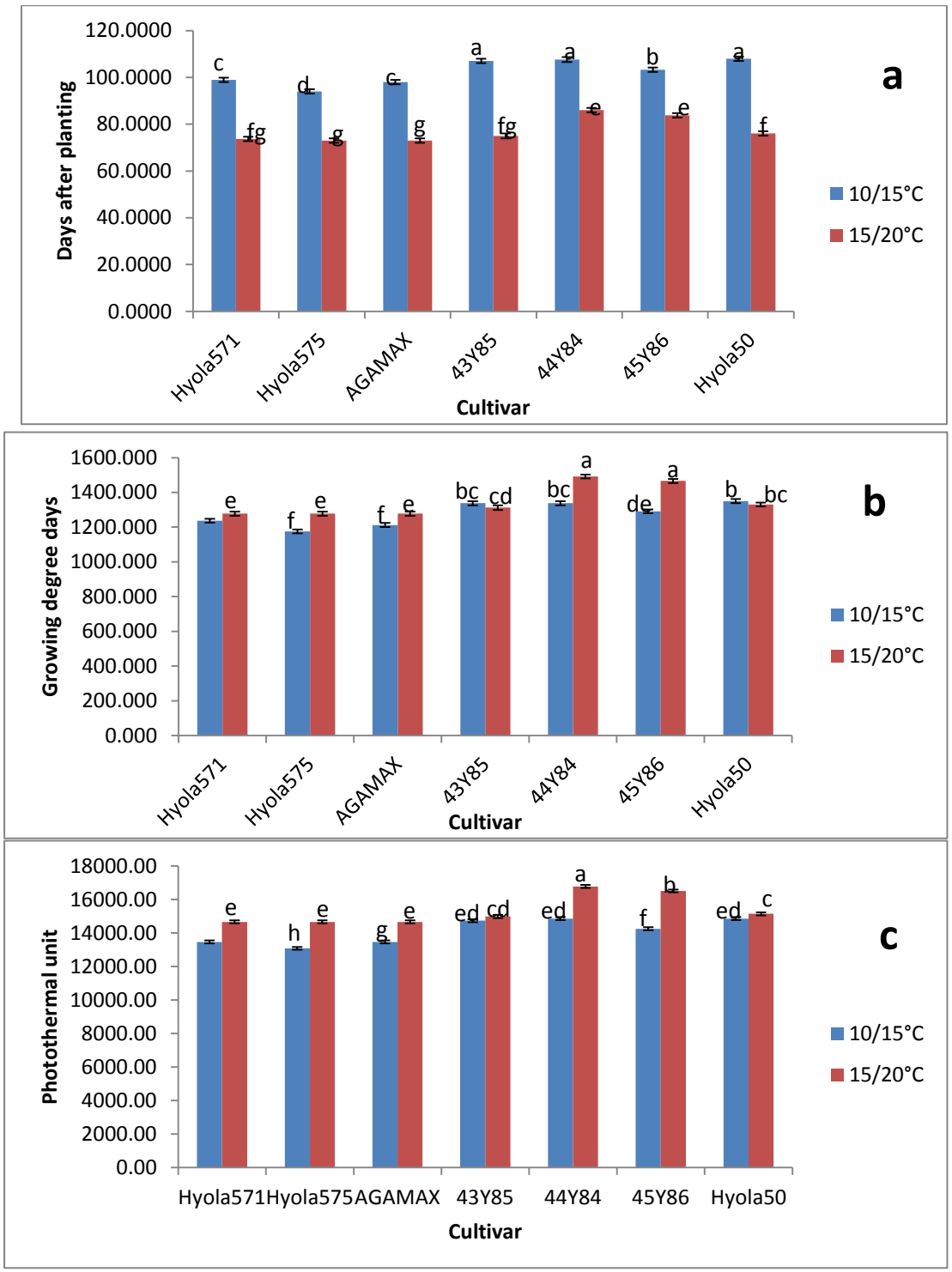

Figure 12 Effect of temperature on a) the number days, b) growing degree days (degree-days) and c) photothermal unit (degree-hour-days) required from planting till seed ripening of different cultivars. Values/ bars with the same alphabetical lettering do not differ significantly at P=0.05

5.3.4 Physiological maturity

Number of days, GDD and PTU required by cultivars from planting to physiological maturity (growth stage 5.4) at 10/15^{0}C and 15/20^{0}C temperature regime; are shown by Figure 13.

Cultivars required significantly more days from planting to the physiological maturity stage when grown at 10/15^{0}C than at 15/20^{0}C (Figure 13a). On average about 141.29 days were required from planting to physiological maturity a temperature of 10/15^{0}C, with cultivar 44Y84 requiring significantly more days than other cultivars. Hyola 50 and 45Y86 required more days than early maturing Hyola 571, Hyola 575, AGAMAX and 43Y85. At the 15/20^{0}C temperature regime, 113.20 days were required on average, with a similar trend between cultivars except for no significant difference between 44Y84 and 45Y86. .

In contrast to number of days, GDD requirement from planting to physiological maturity were significantly more at the 15/20^{0}C temperature regime compared to 10/15^{0}C (Figure 13b). On average cultivars required 1981.04 degree-days from planting to physiological maturity at 15/20^{0}C. Differences do exist between cultivars, with 44Y84, with the exception of 45Y86, requiring significantly more GDD than other cultivars. Hyola 50 also requires more GDD than early maturing Hyola 571, Hyola 575, AGAMAX and 43Y85. At the 10/15^{0}C temperature regime, cultivars required on average 1766.07 degree-days from planting to physiological maturity and differences between cultivars showed a similar trend than for 15/20^{0}C.

The PTU requirement from planting to physiological maturity showed a similar trend than GDD with significantly more PTU required at 15/20^{0}C than at 10/15^{0}C (Figure 13c). On average, 21811.29 degree-hour-days were required at the 15/20^{0}C temperature regime. As in the case of GDD, 44Y84, with exception of 45Y86, required significantly more PTU than other cultivars, while Hyola 50 also required more PTU than early maturing Hyola 571, Hyola 575, AGAMAX and 43Y85. At the other, at the 10/15^{0}C temperature regime, 18404.86 degree-hour-days were required, on average, and differences between cultivars were similar to that at the higher temperature regime. .

At physiological maturity an increase in night/day temperatures from 10/15^{0}C to 15/20^{0}C reduced number of days, but increased the GDD and PTU requirement of all cultivars tested. Significant differences were recorded between cultivars, with mid maturing cultivars 44Y84, 45Y85 and to a lesser extend also Hyola 50, requiring significantly more days, GDD and PTU from planting to reach physiological maturity than early maturing Hyola 272, Hyola 575, AGAMAX and 43Y85.

The same trends of cultivar responses to the two temperature regimes, with regard to number of days, GDD and PTU, were observed as at budding, flowering and seed ripening with the exception that cultivar 43Y85, which behave similar to mid maturing cultivars at earlier growth stages, suddenly confirms its classification as an early maturing cultivar. It is also noteworthy that this particular cultivar shared most of the morphological and physiological characteristics of mid-maturing types, but only seem to have a shorter pod filling period. It appeared that 43Y85 has a unique physiological mechanism of rapid seed-filling and ripening processes, which enabled it to catch up with early maturing cultivars after sharing the physiological trait(s) for lateness from germination to the beginning of seed-filling.

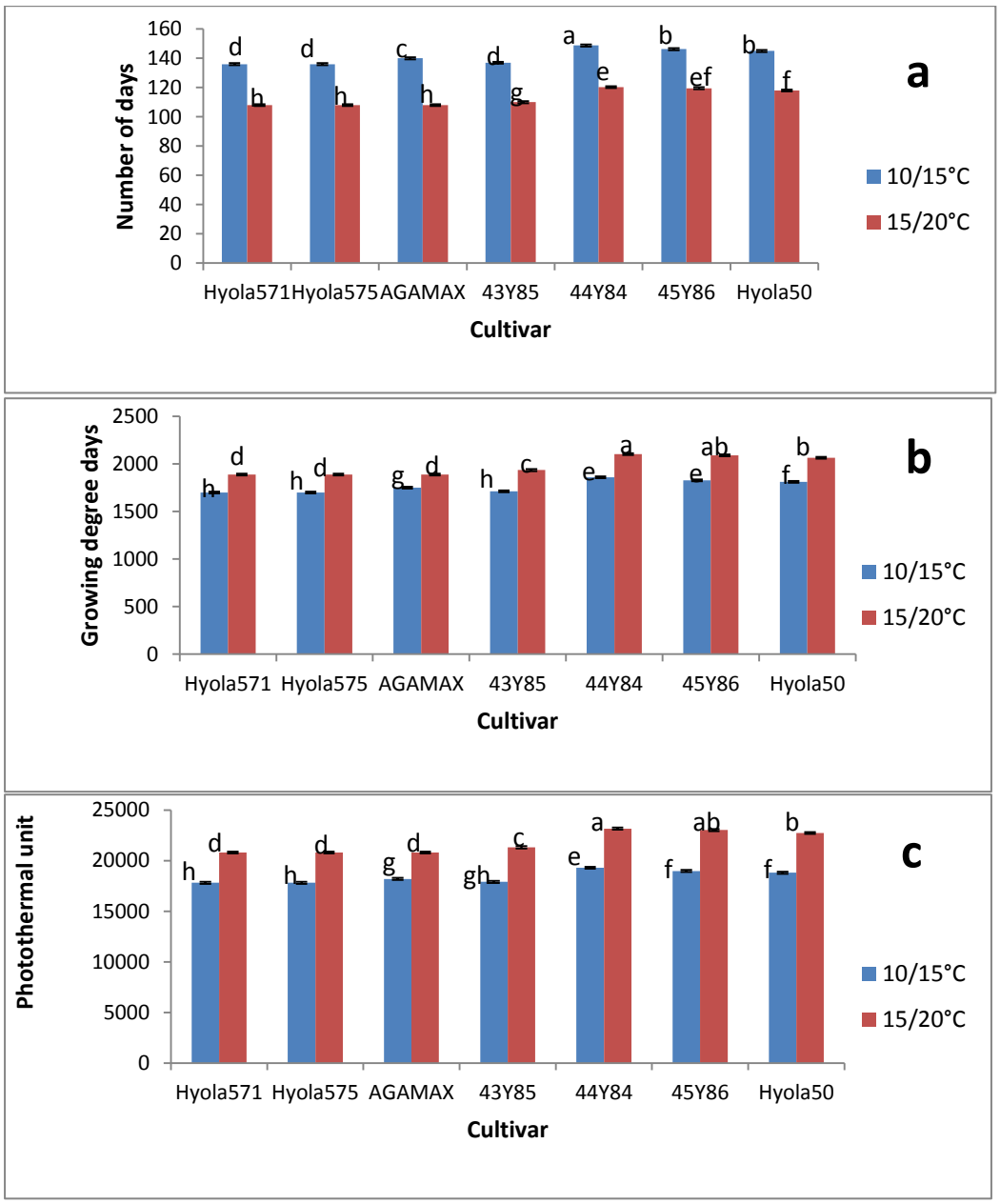

Figure 13 Effect of temperature on a) the number days, b) growing degree days (degree-days) and c) photothermal units (degree-hour-days) required from planting till physiological maturity of different cultivars. Values/ bars with the same alphabetical lettering do not differ significantly at p=0.05

5.4 Simple relationships between DAP, GDD and PTU and plant components at budding, flowering and final harvest stages.

Days after planting (DAP), growing degree days (GDD) and photothermal unit (PTU) were correlated with leaf area (cm^2), dry mass (g), number of pods ($plant^{-1}$) and pods dry mass (g) at budding, flowering and final harvest to establish whether there were relationships between DAP, GDD, PTU requirements and mentioned plant growth components.

In general poor correlations were shown between physiological parameters (DAP, GDD and PTU) and plant components (Table 2). This was especially true for correlations between GDD as well as PTU with plant components. In both cases correlation coefficients (r-values) did not show any trend with regard to plant growth stages (planting to budding, planting to flowering or planting to final harvest) and negative r-values were recorded for most plant components. This somewhat surprising result may be ascribed to the negative effects of the higher temperature regimes on most plant components, while the higher temperature regime resulted in increase in GDD and PTU. Data from both temperature regimes were combined (because of the limited data points) to determine the relevant relationships and stronger correlations should be possible if enough data is available to do correlations for specific temperature regimes.

Correlations between the number of days after planting and plant components were generally positive and did show improving r-values with time (growth stage of the crop). The best correlations of r= 0.7259; r= 0.6097 and r= 0.5566 were shown between number of days to final harvest and plant dry mass (DM), pod dry mass (PDM) and number of pods per plant (NPP).

The implication of these results is that as number of days from planting to final harvest increase dry mass, number pods ($plant^{-1}$) and pods dry mass at final harvest of canola cultivars increase. Contrastingly, increased GDD and PTU, decreased total above ground DM, number of pods ($plant^{-1}$) and pods dry mass at final harvest. Number of days from plant to final harvest (length of growth period or maturity grouping) can for this reason used to predict final dry mass production as well as number of pods per plant and pod dry mass, which should be indicative of grain yield potential.

Table 2 Simple relationships between number of days after planting (DAP), growing degree days (GDD), photothermal unit (PTU) from planting to budding (BD), planting to flowering (FL) and planting to final harvest(FH) and leaf area (LA), dry mass (DM), number of pods plant^{-1} (NPPP) and pod dry mass (PDM) as quantified by correlation coefficient (r) values.

DAP	BD	FL	FH
LA	-0.2311	0.3922	0.4822
DM	-0.3582	0.4320	0.7259
NPPP	0.4606	0.4619	0.5566
PDM	0.4884	0.53323	0.6097
GDD	**BD**	**FL**	**FH**
LA	0.2860	0.0076	-0.1371
DM	0.4926	-0.6316	-0.5056
NPPP	-0.6227	-0.5947	-0.6013
PDM	-0.6329	-0.5750	-0.5385
PTU	**BD**	**FL**	**FH**
LA	0.3257	0.5835	-0.2240
DM	0.5085	-0.0599	-0.5945
NPPP	-0.4991	-0.6113	-0.6400
PDM	-0.5610	-0.5845	-0.5989

Conclusions

The results showed that increasing daily mean temperature from 12.5^{0}C to 17.5^{0}C , on average, reduced the duration of the vegetative growth phase of canola cultivars by 3.79 days, flowering time by 10.38 days, time to beginning of seed-filling by 25.39 days and from planting to physiological maturity by 28.09 days. These reductions in the duration may however change if plants were grown at different day length Increased GDD and PTU due to higher mean daily temperatures. However, the reduction in duration decreased the total above ground dry mass, number of pods (plant^{-1}) and pods dry mass at final harvest.

In general, the results indicate that mid maturing cultivars, Hyola50, 45Y86 and 44Y84 and interestingly early maturing 43Y85 responded in a similar manner during early growth stages, while Hyola 571, Hyola 575 and AGAMAX responded alike at both temperature regimes with respect to number of days, GDD and PTU. The mid-maturing cultivars and 43Y85 required more days, GDD and PTU from planting date to each of the growth stages studied. However, when looking at the requirements to physiological maturity, 43Y85, responded like an early-maturing cultivar, as it was classified.

Therefore, it can be concluded that cultivars responded differently to night/day temperature regimes of 10/15^{0}C and 15/20^{0}C with respect to number of days, GDD and PTU from planting to germination, first true leaf appearance, flowering, seed ripening and physiological maturity. Cultivars with intrinsic trait(s) for lateness tend to require more number of days, GDD and PTU from planting to these growth stages. Increases in night/day temperatures from 10/15^{0}C to 15/20^{0}C reduces number of days from planting date to all the growth stages and with exception of vegetative growth phase, increased GDD and PTU at all growth stages studied.

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CHAPTER 6

Summary /General Conclusions

The effect of temperature on crop phenology has been extensively studied, but little is known about the effect of temperature on growth, yield and phenological responses with regard to the required number of days, growing degree days (GDD) and photothermal units (PTU) required by canola to reach specific growth stages in the South African production areas.

To evaluate the effect of temperature on phenological responses of canola cultivars with respect to required number of days, growing degree days and photothermal units required to reach specific growth stages, seven canola cultivars selected from early- and mid-maturing groups (early = Hyola 571 CL, Hyola 575 CL, AGAMAX and 43Y85; mid maturing = 44Y84, 45Y86 and Hyola 50) grown in the Western Cape canola production area of South African were selected. These cultivars were grown in 3 litre plastic bags filled with a mixture of sand and compost at ratio of 1:1 and irrigated with fully balanced nutrient solution (2.0 EC) in two glasshouses at night/day temperature regimes of 10/15^{o}C and 15/20^{o}C. Crops were planted on 11 February 2014 and the final harvest was done on 14 July 2014 with the result that the day length varied between 13:20 hours at planting and 10:48 hours during the final harvest. Number of days from planting to seedling emergence, first true leaf appearance (2.1), budding (3.1), first flower opening (4.1), seed ripening (5.1) and seed physiological mature (5.4) stages were recorded. Number of days to each growth stage were multiplied by mean day/night mean temperatures of 12.5^{o}C and 17.5^{o}C to determine the growing degree days (GDD) required by a cultivar to reach different growth stages at each temperature regime. There-after GDD were multiplied by the mean day length (number of hours of sunshine) to determine the photothermal requirements of different cultivars at each temperature regime. Plant heights were measured at 14 days-intervals at 28, 42, 56, 70 and 84 days after planting. Number of leaves (plant^{-1}) at budding stage were determined, leaf area (LA in cm^{2}), above ground dry mass (DM) g (plant^{-1}) at budding, flowering and physiological maturity stages were determined. Number of flower stems and pods (plant^{-1}) were counted at seed physiological maturing stage. PGR was determined at (from planting to budding, budding to flowering, and flowering to physiological maturing) stages. RGR and NAR were also determined from budding to flowering and flowering to physiological maturing stages. DAP, GDD and PTU at budding, flowering and physiological maturing stages were correlated with LA, DM, NPP and PDM at budding, flowering and physiological maturing stages to determine whether there were relationships between the variables.

Effect of temperature on morphological and reproductive development of different canola cultivars

The study showed that by increasing night/day temperature from 10/15^{0}C to 15/20^{0}C plant height, number of leaves (plant^{-1}) at budding stage, leaf area at budding , plant growth rate (PGR) from planting to budding stage and relative growth rate (RGR) from budding to flowering stage were increased. However, PGR from budding to physiological maturity, RGR from flowering to physiological maturity, net assimilation rate (NAR) from budding to flowering stage, leaf area at flowering and physiological maturity stages , as well as number of flower stems, number of pods (plant^{-1}), above ground total dry mass at flowering and physiological maturity stages were decreased. Pod dry mass at physiological maturity decreased by 22.24% to 40.35% for different cultivars which clearly demonstrated the sensitivity of canola cultivars to increasing night/day temperatures.

The results also showed that on average, later maturing cultivars (mid-maturing), produced more leaves at budding stage, leaf area at budding as well as flowering and physiological maturity stages when compared to early maturing cultivars. Above ground dry mass of mid maturing cultivars were also higher at budding stage, but not at flowering and physiological maturity stages. At physiological maturity stage, early maturing cultivars such as Hyola 575 CL and Hyola 571 CL) showed higher reductions in pod dry mass than later (mid) maturing cultivar Hyola 50 with an increase in night/day temperature from 10/15^{0}C to 15/20^{0}C. This results indicate that Hyola 50 might be more heat tolerant than early maturing Hyola 571 CL and Hyola 575 CL. Surprisingly, early-maturing 43Y85 shared most of morphological characteristics of mid-maturing types from the same breeding company, such as 44Y84 and 45Y86 instead of early types such as Hyola 571 CL and Hyola 575 CL from a different breeding company. This might indicate that morphological characteristics are to a large extend be determined by the genes used by different breeding companies.

Effect of temperature on the phenological responses of different canola cultivars

This study showed that by increasing the mean daily mean temperature from 12.5^{0}C (10/15^{0}C night/day) to 17.5^{0}C (15/20^{0}C night/day) the duration of the period from planting to seedling emergence of seven canola cultivars tested, decreased on average by 1.27 days from 6.143 days to 4.875 days. The vegetative growth phase (planting till budding) decreases on average by 3.79 days from 42.5 days to 38.71 days. The period from planting till flowering (first flowers appear) on average by 10.32 days from 60.32 days to 50 days. On average the period from planting to physiological maturity was decreased by 28.09 days from 141.29 days to 113.20 days due to the increase in temperatures from12.5^{0}C (10/15^{0}C night/day) to 17.5^{0}C (15/20 ^{0}C night/day).

With the exception of vegetative growth stage, GDD and PTU requirements to reach specific growth stages increased with an increase in temperature. On average the GDD

and PTU requirements to reach budding stage decreases from 677.5 to 529.91 degree-days and from 8398.59 to 5705.63^{0} degree-hour-days. Similarly the requirements to reach flowering stage decreases from 871.25 to 754.09 degree-days and from 10651.29 to 9096.09 degree-hour-days. To reach physiological maturity, 1766.07 degree-days and 18404.86 degree-hour-days were required on average at the 10/15^{0}C temperature regime, while on average, 1981.04 degree-days and 21811.29 degree-hour-days were required at the 15/20^{0}C temperature regime. Plant growth parameters such as dry mass, leaf area, number of pods (plant^{-1}) and pod dry mass (plant^{-1}) at specific growth stages showed a positive correlation with the number of days needed to reach that growth stage, but not with GDD or PTU requirements.

Although cultivar differences with regard to the number of days required to reach specific growth stages were in line with their maturity grouping (early or mid-maturing), differences in GDD and PTU during all growth stages, except for physiological maturity, cannot be explained by their maturity grouping, because early maturing 43Y85 responded similarly to mid-maturing Hyola50, 45Y86 and 44Y84. However, at physiological maturity number of days needed, GDD and PTU requirements were in line with their maturity grouping with early maturing Hyola 571CL , Hyola 575 CL, AGAMAX and 43Y85 needing less days, GDD and PTU compared to mid-maturing 44Y84, 45Y86 and Hyola 50.

These results indicate that number of days, GGD and PTU requirements to reach physiological maturity may be used to describe the cultivar maturity groupings, but because of the effect of temperature and day length, GDD and PTU should be more accurate. More research is however needed to determine the effect even higher temperature regimes and especially the effect of different day lengths might have. Because all cultivars grown in South Africa at present can be described as early to mid-maturing cultivars, differences between cultivars were small and value could be added if late maturing cultivars could be included in future research.