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CONSTRAINTS TO CARROT SEED PRODUCTION IN NEW ZEALAND

A thesis presented in partial fulfilment of the

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Abstract

New Zealand is one of the largest producers of carrot seeds globally. However, carrot seed production is increasingly vulnerable to the effects of climate change, which may force the geographical shifts in cultivation locations. These shifts increase the possibility of genetic contamination from wild carrots, which could have a consequential impact on the cultivar purity of carrot seeds. There are limited studies that have explored the impact of climatic factors and wild carrots on carrot seed production within the context of New Zealand. This literature mainly focused on the effect of climate change on floral characteristics of cultivated carrots and management of wild carrots rather than risk of seed contamination or climate interactions specific to wild and cultivated carrots. The overall aim of this thesis is to investigate two key constraints on carrot seed production in New Zealand, especially those caused by climate change and the existence of wild carrots.

A panel data modelling study was conducted to investigate the effects of maximum and minimum temperature, and precipitation during critical phenological stages on carrot seed yield. This modelling study was carried out by using cross-sections from 28 locations within the Canterbury and Hawke's Bay regions of New Zealand that cultivate carrot seed crops and time series from 2005 to 2022. Findings show that there were significant ($p < 0.01$) variabilities in temperature and precipitation across different growing phases, except for precipitation at the vernalization phase. According to the analysis of marginal effects, the highest significant effect of minimum (187.724 kg/ha of seed yield reduction for each 1 °C increment) and maximum temperature (1 °C rise increases seed yield by 132.728 kg/ha), and precipitation (1 mm increment of precipitation declines the seed yield by 1.745 kg/ha) on carrot seed yield were reported at vernalization, and flowering and seed development, respectively. Results from the modelling study conclusively show that carrot seed production will be negatively affected by climatic change. Meanwhile, the germination phase, including seed germination and seedling

emergence, is extremely sensitive to adverse temperature, particularly temperatures above the optimum, conditions and represents a critical stage for the successful establishment of seed crops. However, further studies were needed to accurately determine the impact of temperature on the germination of carrot seeds, including wild and cultivated carrots.

Therefore, germination experiments were carried out to investigate how extreme temperature can affect the seed germination of carrot male line and female line, and wild carrots by using a temperature gradient plate. The findings indicated that the germination percentage, mean germination time, and time required for 50 % germination of wild and cultivated carrots can be significantly ($p < 0.05$) affected by the interaction effects of temperature and genotypes. The highest (87 %) and rapid germination (6.8 days) of wild carrots was observed at 21 °C and 25 °C, respectively. The highest percentage of germination was recorded at temperatures of 20 °C for cultivated carrots, including male (98 %) and female (97 %) lines; however, these differences were not statistically ($p > 0.05$) significant. The exponential model was chosen based on statistical criteria to determine the base, optimal, and ceiling temperatures for the seed germination of wild and cultivated carrots. The values of base, optimum, and ceiling temperatures of wild, and cultivated carrots ranged from -0.22 to 2.98 °C, 22.11 to 25.55 °C, and 37.88 to 38.64 °C, respectively. According to the climate change projections, the germination rate (GR₅₀) of wild and cultivated carrots is predicted to increase along with the increasing temperature. Given the comparatively increasing germination rate of wild carrots under projected temperature increments, it is important to manage their vegetative growth and development efficiently. However, further investigations are required to precisely determine the most effective timing and growth stage for managing wild carrots.

Consequently, a glasshouse experiment was conducted to compare and model the vegetative growth pattern of different morphological traits, such as plant height, leaf number, root diameter and length, and shoot and root fresh and dry weight, in both wild and cultivated

carrots, to understand appropriate weed management strategies with respect to their growth stages. Studying the vegetative growth pattern of wild carrots helps determine the most appropriate growth stages for implementing effective weed control methods, such as timing of herbicide application or mechanical control. This study comprised two main factors; 1. Genotype (T_1 : cultivated and T_2 : wild carrots) and 2. Length of juvenile phase, defined as the time duration between sowing and initiation of vernalization (J_1 : 12-week, J_2 : 8-week, and J_3 : 4-week). The morphological traits studied included plant height, leaf number, shoot fresh and dry weight, root fresh and dry weight, root diameter and root length. The recorded data were analyzed using analysis of variance (ANOVA), correlation, and regression analysis, and principal component analysis (PCA). The interaction effect between ‘genotype \times juvenile stage’ has shown a significant ($p < 0.05$) effect on all the traits except plant height. Shoot and root growth of wild carrots exhibited rapid growth after reaching 8-week juvenile stage (9-11 leaves stage). Results from correlation and regression analysis, especially power regression, indicated that the above-ground morphological traits can be used to determine the characteristics of below-ground parts of both wild and cultivated carrots. PCA presented that morphological characteristics, except plant height, can be used to differentiate wild and cultivated carrots. According to the findings of this study, it is clear that wild carrots grow more rapidly than cultivated carrots. Therefore, it is important to manage the wild carrots at their early growth stages, especially prior to the flowering. Meanwhile, further studies are required to compare and understand the reproductive phase of wild and cultivated carrot genotypes found in New Zealand.

Therefore, an experiment was executed to evaluate the effect of different juvenile phases (J_1 - 12 weeks, J_2 - 8 weeks, and J_3 - 4 weeks), and vernalization phases (V_1 - 12 weeks, V_2 - 4 weeks, and V_3 - no vernalization) on floral characteristics and flowering behaviour of cultivated (G_1) and wild (G_2) carrots, to understand the life history strategies of both wild and cultivated

carrots. The findings indicated that the interaction effect between $G \times J \times V$ on the percentage of flowering and time required for flowering was significant ($p < 0.05$). Cultivated carrots flowered only under treatments with 12-week vernalization, whereas wild carrots exhibited 100 % flowering across all treatments. Overwintering survival was comparatively higher for wild carrots (94.9 % - 100 %) than cultivated carrots (66.1 % - 98.3 %), likely due to their higher cold stress tolerance and deeper root systems. This study also shows that wild carrots can establish themselves as either summer annual or winter annual in New Zealand, whereas commercial carrots may only be cultivated as biennials for seed production.

The overall findings of this doctoral research demonstrate that climate change can have a significant impact on carrot seed production in New Zealand. As a result, shifting the production regions to wild carrot-prone locations can detrimentally affect the genetic purity of the cultivated carrots since wild carrots can establish as a winter annual and summer annual, and have a strong capability of surviving over the winter. Therefore, it is important to control the wild carrot prior to the flowering, especially at their early growth stages. Further research is recommended to investigate the contribution of pollinators on pollen flow from wild to cultivated carrots and to determine the optimum isolation distance by incorporating the factors like range of pollinators, climatic factors, and density of the wild carrot population.

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List of Abbreviations

%	Percentage
ABA	Abscisic acid
ADF	Augmented Dickey-Fuller
AHEAD	Accelerating Higher Education Expansion and Development
AIC	Akaike information criterion
ANOVA	Analysis of variance
BIC	Bayesian information criterion
CMS	Cytoplasmic male sterile lines
CPE	Cumulative pan evaporation
CSGS	Carrot seed crop growing season
CWR	Crop wild relatives
Eq	Equation
F1	First filial generation
FAR	Foundation for Arable Research
FC	Field capacity
FGP	Final germination percentage
g	grams
GA	Gibberellic acid
GCM	General Circulation Model

gL ⁻¹	gram per litre
GM	Genetically modified
GR ₅₀	50 % of the germination rate
ha	Hectare
ISTA	International Seed Testing Association
K	Potassium
kg	Kilogram
km	Kilometer
KNO ₃	Potassium nitrate
LSD	Least significant difference
Mg	Magnesium
MGT	Mean germination time
mM	Millimolar
MPa	Megapascal
N	Nitrogen
NaCl	Sodium chloride
NIWA	National Institute of Water and Atmospheric Research
NZ	New Zealand
OFCNZ	Our future climate New Zealand
PCA	Principal component analysis

PCs	Principal components
PGU	Plant growth unit
PRISMA	Preferred Reporting Items for Systematic Reviews and Meta-Analyses
PVC	Polyvinyl chloride
R ²	Coefficient of determination
RCBD	Randomized complete block design
RCP	Representative Concentration Pathways
RMSE	Root mean square error
SIRC	Seed Industry Research Centre
SSPs	Shared Socioeconomic Pathways
t	ton
t ₅₀	Time to reach 50 % germination
TGP	Temperature gradient plate
TT	Thermal time
UN	United Nations
USD	U.S. dollar
WHO	World Health Organization

Chapter 1: General Introduction

1.1 Background to constraints relating to carrot seed production in New Zealand

New Zealand, one of the world's top seed producers, supplies around 50 % of carrot (*Daucus carota* L. subsp. *sativus*) seeds to the global market (Preece, 2023; Trivedi et al., 2009). This is mainly due to New Zealand's reputation for the consistent production of high-quality seeds. Furthermore, New Zealand is an ideal location for seed production in the counter-season when the northern hemisphere experiences the winter (Mckay, 2008). Seasonal variations allow for the production of carrot seeds in New Zealand, where a cool winter climate is necessary to induce the flowering of carrots (Wohlfeiler et al., 2021). According to Trivedi et al. (2009), F1 hybrids are the most common type of carrot seed grown in New Zealand for export to foreign clients. The export value of carrot seeds was \$24 million in 2021 (2010: \$7.6 million). The primary export market for carrot seeds is Europe with a value of \$23 million exported to the European continent in 2021 (Aitken & Warrington, 2021). Moreover, the majority of carrot seed production is centered in the Canterbury region located on the South Island. However, carrot seed producers want to expand carrot seed production in the North Island of New Zealand, especially in the Hawke's Bay region (Bhatia, 2023). To achieve this, New Zealand needs to address the constraints related to climate change and genetic contamination from the wild carrot (*Daucus carota* L. subsp. *carota*) on carrot seed production. Both these issues limit the extent of suitable land area for the establishment of carrot seed crops in New Zealand.

The seed industry is one of the most climate-sensitive sectors, with several phases of seed production heavily relying on the climatic conditions during the crop's whole life cycle (Moharana et al., 2023). Among those, temperature and precipitation are the two key climatic factors that can

significantly affect seed production (Maity et al., 2023). According to climate change projections (mid-range estimations), New Zealand's temperatures are predicted to rise by 0.8 °C by 2040, 1.4 °C by 2090, and 1.6 °C by 2110 (compared with 1986–2005). Furthermore, more variety in precipitation amounts and periodicity is expected for New Zealand than in forecast temperature changes; thus, predicting the pattern of precipitation is very challenging (Mullan et al., 2018). There will also be a noticeable reduction in the number of cold nights, which is anticipated to decline by 30 % to 90 % by 2090 (Climate Change Adaptation Technical Working Group, 2017). Furthermore, Heath (2021) stated that the eastern regions of New Zealand's North and South Islands, where the majority of the farms for the production of carrot seeds are located, will become drier during the winter and spring and more rainy during the summer. It is also anticipated that New Zealand's drought and flooding will become more severe (Booth et al., 2020).

The climatic conditions have a substantial impact on the phenological phases of the carrot seed crop (Broussard et al., 2017; Deleuran & Boelt, 2009; Dias et al., 2015). For example, a low temperature (5 °C for 11 to 12 weeks) is an unavoidable requirement for the vernalization and induction of flowering in carrots, emphasizing the importance of winter temperature in carrot seed production (Atherton et al., 1990; Linke et al., 2019). Furthermore, a rise in temperature may have an impact on the floral components of carrot flowers, including their nectar content, volatiles, and pollen viability, which may alter the pollinators' foraging behaviour (Broussard et al., 2017). Similarly, the quantity and quality of carrot seeds can be also substantially decreased by higher temperatures during pollination, fertilization, and the early stages of seed development (Elballa & Cantliffe, 1996). Although carrot seed crops in New Zealand are irrigated, decreased precipitation can still affect soil moisture dynamics, potentially affecting the development of high-quality taproots (Jagosz et al., 2019; Reid & Gillespie, 2017). It is evident from existing research that the

predicted climate changes in New Zealand will have a significant effect on the country's carrot seed production. To overcome this issue, it will be necessary to geographically shift the locations where carrot seed production takes place to areas with the optimal environment for the growth of carrots, such as locations in Hawke's Bay region, though in some cases, invasive wild carrot species might be a risk in these new locations (Hauser & Bjørn, 2001).

Wild carrot is a problematic weed in hybrid carrot seed-producing crops. Wild carrot is observed in wastelands and roadsides, especially adjacent to carrot seed-producing sites (Hauser & Shim, 2007; Rome & Lucero, 2019). Similar observations have been reported in New Zealand, which is why wild carrots are considered an emerging significant problem to carrot seed production (Bhatia, 2023). Wild and cultivated carrots are sexually compatible, enabling hybridization between them (Schouten et al., 2002). Thus, cultivar purity in carrot seed lines can be reduced due to gene flow between wild and cultivated carrot (Rong et al., 2010), resulting in the production of white taproots rather than orange from commercial carrot seeds (Hauser et al., 2004). In addition, using genetically impure (wild \times cultivated) carrot seeds results in early bolting of carrots being produced for consumption, which is undesirable for the production of high-quality edible taproots (Wijnheijmer et al., 1989). Consequently, it is vital to control the wild carrots before they flower in order to eliminate or minimize the pollen transfer from wild to cultivated carrots (Dyer, 2020; Webster et al., 2003). This implies the importance of studying the vegetative and reproductive growth of wild carrots. Furthermore, site-specific experiments must be conducted to formulate control strategies of wild carrots since the life history of the wild carrot (annual, biennial, or perennial) varies depending on the geographical regions (Mandel & Brunet, 2019).

Despite the fact that the global supply of high-quality carrot seeds depends on the production of carrot seeds in New Zealand, limited research has been done to address impacts of climatic

variability and genetic contamination from wild carrots. There is a significant research gap in determining how climate change and the pollen flow of wild carrots will affect the production of carrot seeds in New Zealand. The research presented in this thesis was directed by the need to understand the impact of climatic factors, especially temperature and precipitation, on carrot seed production and to recommend weed management strategies to control wild carrots via understanding the vegetative growth and flowering pattern of wild carrots. This will make it easier for the industries that produce carrot seeds in New Zealand to increase both the quantity and quality of the seeds by choosing optimal locations, considering climatic conditions and presence of wild carrot populations.

1.2 Research objectives

The main objective of the study is to examine two important constraints to the production of carrot seeds in New Zealand, particularly those caused by climate change and wild carrot presence.

The specific objectives that supported the main objectives were as follows:

1. To study the impact of climate change from 2005 to 2022 on carrot seed yield in New Zealand by identifying the pattern of changes in maximum and minimum temperature, and precipitation at different phenological stages of carrot seed crop.
2. To model the germination of carrot male and female lines, and wild carrots across a temperature gradient.
3. To compare the morphological traits of wild and cultivated carrots via modelling the vegetative growth pattern of both types of carrots.

4. To determine the interaction effects between juvenility and vernalization on flowering and floral characteristics of wild and cultivated carrots and to determine the life cycle and floral morphology of New Zealand wild carrots.

1.3 Thesis format

This thesis consists of seven chapters. Chapter 1 is the general introduction which comprises background information on the constraints faced by the carrot seed producers in New Zealand and the main and specific objectives of the thesis. Chapter 2 is a literature review that describes the projected climate change in major seed-producing regions (Canterbury and Hawke's Bay) in New Zealand, the impact of these climatic changes on the vegetative and reproductive phases of carrot seed crops, distribution of wild carrots in New Zealand, genetical contamination between wild and cultivated carrots and practical solutions for these significant constraints. Chapters 3 to 6 are experimental chapters, prepared as journal articles comprised of an abstract, introduction, materials and method, results and discussion, and conclusions. **Therefore, concepts of these studies may be repeated throughout the thesis.** The general discussion of the research is in Chapter 7.

Chapter 2: Literature Review

This chapter presents a comprehensive review of the literature to give context to the primary objectives of this thesis as discussed in Chapter 1. Climate change is a vital challenge to carrot seed production. As a result, there are significant possibilities of having to shift carrot seed production sites to climate-optimal regions. However, these optimal locations may also have higher infestation of wild carrots, increasing the risk of genetic contamination. In order to address these issues, this review comprises the following sections:

- a. Impact of climate change on carrot seed production (2.1)
 - i. Effect of climate change on global food and seed security
 - ii. Phenology of carrot seed crops
 - iii. Projected climate change in major carrot seed-producing regions in New Zealand
 - iv. Effect of extreme climatic factors on different phenological phases of carrot seed crop
- b. Wild carrots and their influence on quality carrot seed production (2.2)
 - i. Resilience of wild carrots to the extreme climatic conditions
 - ii. Pollen flow from wild to cultivated carrots
 - iii. Geographical distribution of wild carrots
 - iv. Weed management strategies to control the wild carrots adjacent to the carrot seed-producing sites

This literature review provides a comprehensive insight into the above sections, which will further assist in finding the significant research gaps present in the existing literature.

2.1 Impact of climate change on carrot seed production

2.1.1 Influence of changes in climatic conditions on food and seed security

Climate change and the exponential increase in human population are the most significant factors that threaten global food security (Coronado-Apodaca et al., 2023; Mirzabaev et al., 2023). Under the UN's high fertility scenario, Ritchie et al. (2023) predicted that the 7.91 billion people on the planet now will increase to 14.81 billion by 2100. The average temperature and precipitation have changed significantly since the early 1980s, reflecting ongoing changes in the global climate (Kogan, 2022). Agache et al. (2022) stated that based on projections from several global warming scenarios the future global temperature is predicted to rise by 1.5 to 4.4 °C by 2100. Furthermore, previous studies indicated that the dry climates across the world will become drier due to excess evaporation and wet zones become wetter from intensified precipitation. These precipitation projections strengthened drought effects and flooding extremes in dry and wet regimes, respectively (Konapala et al., 2020). Since climate factors directly affect plant growth and development, crop production is mostly reliant on optimum climatic conditions; therefore, global food production can be compromised by climate change (Semeraro et al., 2024). According to a simulation study, crop yield losses could range from 7 % to 23 % under the worst-case scenario of climate change and in the absence of adaptation strategies (Rezaei et al., 2023). These can cause severe threats to global food security and result in serious competition for food (Alaanuloluwa et al., 2020; Hosseini et al., 2024).

Seed security is a vital component of global food security, as seeds are an essential input for crop production (Haug et al., 2023). The availability of sufficient quantities of high-quality seeds of desirable crop varieties at any time and in various cropping seasons is generally known as seed

security (FAO, 2016). Furthermore, seed security is one of the important factors for the sustainability of crop production as it ensures farmers' access to the seeds for crop establishment regardless of climatic conditions and other external factors (Madin et al., 2022). Moreover, Afzal et al. (2019) stated that using high-quality seeds in production systems can enhance agricultural yield by 5-20 %, emphasising the importance of utilising good-quality seeds in relation to resolving challenges with food security. Therefore, seed industries must play a substantial role in guaranteeing the production of high-quality seeds under the threat of climate change (Singh et al., 2013). Seed production is extensively known as one of the agricultural sectors most vulnerable to the impacts of climate change, due to its dependence on particular climatic conditions and sensitive growth phases (Krstić et al., 2023). Globally, elevated temperature and a rise in water stress are considered key factors significantly influencing the reduction of both the quality and quantity of seeds (Hampton et al., 2016). In the midst of climate change, the current global trend implies a continuous rise in demand for a significant amount of high-quality seeds in the future to feed the growing population (Maity et al., 2023).

The limited availability of food and seeds coupled with challenges resulting from climate change can significantly affect the widespread incidence of hunger and malnutrition globally (Nabuuma et al., 2022; Rezvi et al., 2023). Current assessments showed that about 690-783 million people (9-10 %) suffer from hunger, while projections indicate that approximately 600 million (7 %) people will face food insecurity by 2030 (FAO et al., 2023). In the context of malnutrition, the World Health Organisation (WHO) considers vitamin A deficiency in children and pregnant women as one of the most significant global health challenges in low-income nations (Hammaz et al., 2021; WHO, 2024). Furthermore, Pereira et al. (2023) indicated that between 5 and 10 million children suffer from xerophthalmia (early stage of night blindness) each year, with the lack of

consumption of vitamin A-rich dietary sources being the main contributing factor. In addition, consuming foods that contain carotenoids is thought to reduce the chance of various diseases, including cardiovascular issues, cancer, and some illnesses linked to ageing (Dallagi et al., 2023).

2.1.2 Nutritive value of carrots

Globally, carrots are recognized as a key source of carotenoids (Yi et al., 2023). Carotenoids have a significant physiological effect on human nutrition by serving as provitamin A (vitamin A precursors) (Hacke et al., 2023). Carrot consumption is a consistent and growing trend as people become more aware of its health advantages (Singh et al., 2021). To meet the rising demand for carrots, global carrot (including turnip - FAOSTAT combining data for carrots and turnips under one category) production and area harvested have increased by around 86 % and 67 %, respectively between 1961 and 2022 (FAOSTAT, 2024). When seed is the only planting material utilized to propagate and establish carrot seedlings, the demand for quality carrot seed may also rise consequently (Finch-Savage et al., 2001). Furthermore, carrot seed crops, which require two growing phases (juvenile and reproductive phase) to complete their life cycle, are disproportionately susceptible to climate change due to their prolonged phenological growth phases (Godwin et al., 2023). Thus, it is important to investigate the possible effects of extreme climatic conditions on various phenological phases of carrot seed crops and how this could affect the production of quality carrot seeds consequently. Given these facts, it is evident that the impact of climate change on carrot seed production is vital to mitigating future food and seed crises.

2.1.3 Carrot seed production in New Zealand

New Zealand is in Oceania with two main Islands (North and South) divided by Cook Strait and is located in the Southern hemisphere. Furthermore, New Zealand is a major contributor to the global carrot seed market, accounting for approximately 50 % of production. Carrot seed is primarily produced in the Canterbury (Culverden, Methven, Aylesbury, and Darfield) and Hawke's Bay (Hastings, Otane, Ongaonga, and Takapau) regions of New Zealand (Godwin et al., 2023). Therefore, these two regions are the main focus of this thesis. Hawke's Bay and Canterbury regions are located on the Eastern part of the North and South Islands, respectively (**Figure 2.1**).

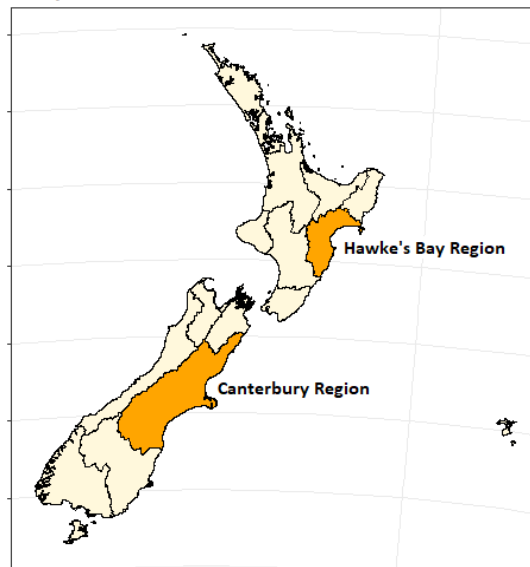


Figure 2.1 Major carrot seed-producing regions in New Zealand,
source: Bhatia (2023)

2.1.4 Phenology of carrot seed crops

Generally, carrot seed crops are grown as biennials to induce the flowering and seed formation processes (Wohlfeiler et al., 2019). In the Southern Hemisphere, countries like Australia, New Zealand, South Africa, and Chile, biennial carrots are sown between January and February (late summer or autumn of the Southern Hemisphere), with the seed harvested between February and March (summer or autumn Southern Hemisphere) of the following year (Christianson, 2014; Howlett, 2012; Wohlfeiler et al., 2019). Similarly, main carrot seed producers in the northern hemisphere, such as Pacific north-west of the USA, southern France, Japan, Israel and Italy, begin sowing seeds in August (late summer of Northern Hemisphere) and harvest seed between August and September (late summer or early autumn of Northern Hemisphere) of the next year (Noland et al., 1988; Spurr & Lucas, 2020; Villeneuve & Latour, 2017). Moreover, a period of low temperature (vernalization) during the winter triggers the switch from the vegetative to reproductive phase and induces flowering, consequently (Spurr & Lucas, 2020). As a result, flowering is most likely to take place between late spring and summer (Davis et al., 2023). Compared with annuals, biennials are exposed to the environment for a longer period of time during the course of their life cycle, indicating a stronger impact of climatic conditions on carrot seed crops (Wohlfeiler et al., 2021). Therefore, it is important to consider the various phenological stages as well as the seasons in which they are occurring (**Figure 2.2**) while investigating the effects of climate change on carrot seed crops.

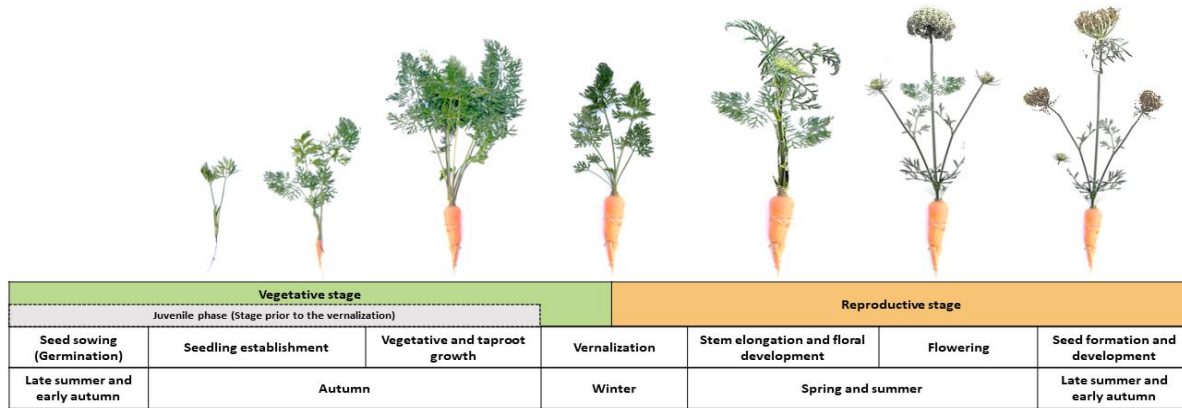


Figure 2.2 Seasonal and phenological phases of the carrot seed crop

2.1.5 Climate change and its trend in New Zealand (Hawke’s Bay and Canterbury)

Figure 2.3 indicates the trend of the projected climate change of Canterbury and Hawke’s Bay regions based on air temperature, precipitation, surface radiation, hot days, wet days, and relative humidity for both RCP 4.5 and 8.5. RCP 4.5 and RCP 8.5 are Representative Concentration Pathways generally used for climate modelling with different greenhouse gas projections, with RCP4.5 denoting a scenario of moderate emissions reductions, whereas RCP 8.5 represents a high-emissions scenario with minimal to no mitigation. Moreover, the results revealed that Hawke’s Bay is predicted to record warmer temperatures than the Canterbury over the year. Precipitation is anticipated to decrease in the Hawke’s Bay region throughout the year under the RCP 4.5 and 8.5 scenarios: however, seasonal precipitation is expected to increase in Canterbury during the autumn, winter, and spring. In addition, the Canterbury region’s summer rainfall is anticipated to decrease in the RCP 8.5 scenario. Under the RCP 4.5 and 8.5 scenarios, the number of hot days in Canterbury and Hawke’s Bay are predicted to increase over the year, except in winter. Furthermore, both the RCP 4.5 and RCP 8.5 scenarios are projected to result in a further decrease in surface radiation in the Canterbury region. In contrast, all seasons-aside from summer under

RCP 4.5 scenario-should see an increase in surface radiation in the Hawke's Bay region. Both the Canterbury and Hawke's Bay regions are predicted to experience a downward trend in relative humidity over the autumn, winter, and spring, with the exception of the autumn (only under RCP 8.5) in the Hawke's Bay region. These results show that the Canterbury and Hawke's Bay regions are most likely to be impacted by the predicted climate change of different seasons, which can have a consequential effect on the production of carrot seeds in New Zealand.

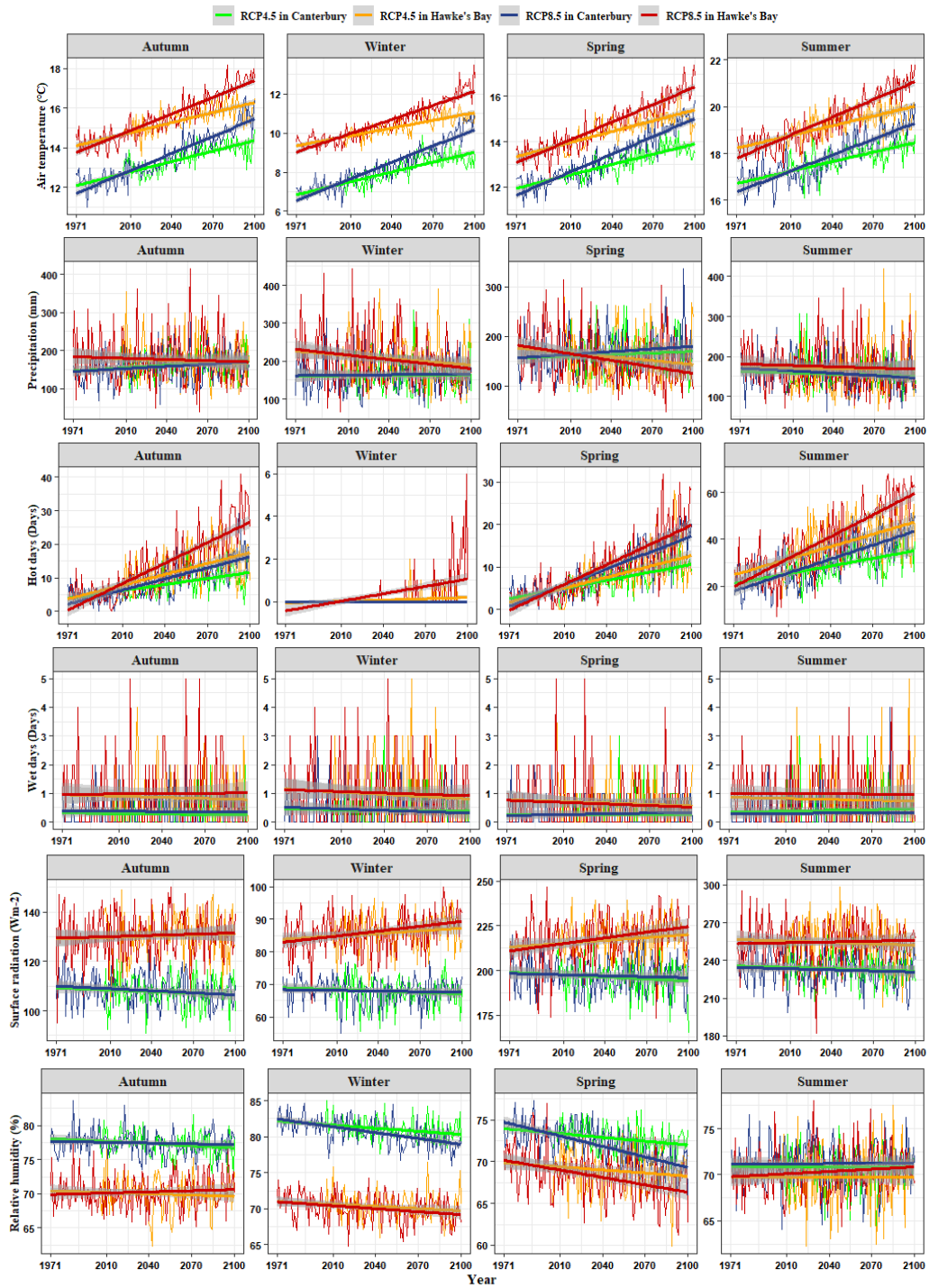


Figure 2.3 Projected changes in seasonal air temperature, precipitation, hot days, wet days, surface radiation, and relative humidity in Canterbury and Hawke's Bay regions, Source: <https://ofcnz.niwa.co.nz/> (2023)

2.1.6 Impact of extreme climatic conditions on the different growth phases of carrot seed crop

2.1.6.1 Juvenile phase

Seed germination is the initial phase in the growth and development of a plant (Vandana et al., 2020). This process begins with the imbibition of water and is followed by the elongation of cells and an increase in cell numbers within a seed (Toole et al., 1956). In regards to climatic factors, temperature and soil moisture are considered the significant aspects that can influence seed germination (Daddario et al., 2017). Low germination due to an increase in stress during the germination period may result in substandard emergence and subsequent heterogeneous growth due to shading of slower emerging plants, which could cause variation in the maturity of the seed crops. Ultimately, the quality of the seed harvested could be reduced due to the lack of synchronization between seed maturity and time of harvesting (Oliva et al., 1988; Tetteh et al., 2018). The germination capacity of carrot seed can be reduced when the temperature exceeds 30 °C, and it can be completely halted in the temperature range between 40-45 °C (Corbineau et al., 1995; Pereira et al., 2007). Increased temperatures can disrupt the metabolic and enzymatic activities that occur during the germination of carrot seeds. Moreover, the optimal temperature range for carrot seed germination has been determined to be between 20 °C and 30 °C (Dias et al., 2015; Nascimento et al., 2008). Seed germination and seedling growth of carrots can be affected by dry conditions caused by deficit soil moisture and fewer rainfall events. These factors can reduce the germination of seeds and seedling emergence by altering the imbibition rate, delaying the mobilization of food reserves and metabolic activities and inhibiting the plumule and radicle elongation (Andriamparany et al., 2020; Schmidhalter & Oertli, 1991). Lada et al. (2004) stated that the optimal soil moisture for the emergence of carrot seedlings is 35-40 % field capacity (FC).

However, a significant decrease in seedling emergence can result if the soil moisture has been maintained above 40 % FC or below 35 % FC. The coinciding of optimum precipitation with the time of radicle initiation and seed germination is advantageous for uniform seedling emergence (Finch-Savage et al., 2001). In contrast, excess rainfall or flooding can reduce the available oxygen in the soil profile, which results in stress and reducing seed germination and seedling emergence (Zhou et al., 2020). Although carrot seed crops in New Zealand are cultivated under irrigated conditions, climate change, particularly fluctuations in rainfall and growing concerns about water availability, can still significantly impact the seed production.

Air temperature is one of the important factors affecting photosynthesis in carrots (Thiagarajan et al., 2012). The optimum range of temperature for photosynthesis and root partitioning of carrots has been reported as 18 °C to 19 °C and 16.5 °C to 19 °C. Furthermore, it has been observed that increasing temperature up to 20 °C increased plant dry weight but that dry weight began to decrease when temperature increased beyond 20 °C (Hussain et al., 2008). Meanwhile, decreasing the temperature below 20 °C leads to photo-inhibitory mechanisms. Due to these mechanisms, photosynthesis can be altered by the fluctuation of air temperature. The shoot and root growth are also adversely affected by the temperature. A temperature increment from 25 °C to 35 °C reduced the shoot and main root dry weights of the *Parano* carrot variety by nearly 43 % and 65 %, respectively (Ibrahim et al., 2006). Likewise, soil moisture also significantly influences the physiological activities and growth and development of plants (Chadha et al., 2019). The predicted increase in global air temperature caused by climate change will impact physiological activities of plants (Dusenge et al., 2019). Due to these effects, the present carrot-producing areas may become unsuitable, whereas the areas, such as locations in Hawke's Bay region, not currently used for carrot production may become possible for the production in future.

2.1.6.2 Vernalization

Climatic factors play a key role in the transition from the vegetative stage to the reproductive stage by initiating various changes to the morphological and physiological processes (Alessandro et al., 2013; Liu et al., 2020; Siswadi et al., 2021). Vernalization is achieved by exposing the plant to low temperatures for a particular period (Slafer et al., 2015). Furthermore, vernalization is a prerequisite for the transition of apical meristems from the vegetative phase to the reproductive phase (Porker et al., 2016; Villeneuve & Latour, 2017).

The juvenile stage of carrots ends when the seedling has initiated 8-12 leaves and the diameter of the carrot taproot is greater than 4 -8 mm (Linke et al., 2019). Strong vegetative growth is important for subsequent seed production, especially for photosynthetic systems and the synthesis of phytohormones (Samuoliene et al., 2009), and the size and formation of taproot (Kumar et al., 2017). Due to the exposure of carrots to cold temperatures, the concentration of gibberellic acid increases within the plant, which stimulates the formation of flowers (Abbas, 2017; Schwab & Neumann, 1975). Genetic mechanisms also influence bolting in carrots by altering the vernalization, photoperiodism, autonomous and floral integrators. The autonomous pathway functions independently of environmental cues. It helps initiate flowering based on the plant's internal signals, whereas floral integrators are genes that act as central hubs, merging signals from different pathways to stimulate flowering (Ou et al., 2017). Wohlfeiler et al. (2021) also observed annuals responded well to the shorter chilling duration than biennials and that most cultivars prefer vernalization at $\sim 5^{\circ}\text{C}$ rather than $\sim 15^{\circ}\text{C}$ for flower formation. The influence of temperature on the rate of carrot flowering was demonstrated by Atherton et al. (1990), who found that increments of temperature from -1°C to 5°C increased flowering, while a significant decline was observed when increasing the temperature from 7°C to 16°C (**Figure 2.4**).

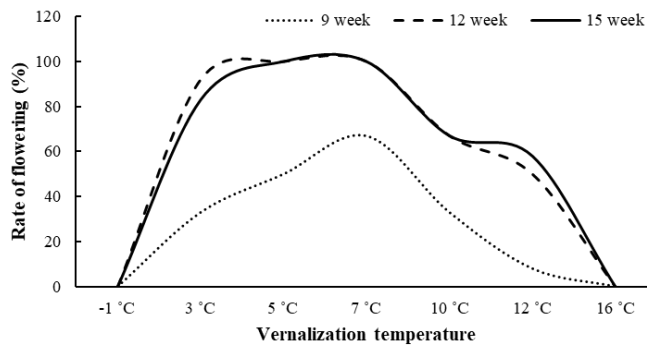


Figure 2.4 Effect of vernalization temperature on rate of flowering; 9, 12, and 15 weeks indicate the duration of chilling period (from Atherton et al., 1990)

2.1.6.3 Floral development

Carrot flower development starts with the formation of a floral stalk, followed by the production of involucre bracts and umbel primordia (Hiller & Kelly, 2019; Linke et al., 2019). Hawthorn (1951) reported carrot seed crops produced from larger stecklings (> 50 mm diameter) flowered and ripened earlier than the smaller stecklings (< 12 mm diameter) by 3 weeks and 1 month, respectively. Quagliotti (1967) observed a significant decrease in flower stalk development when temperature increased from 14 °C to 26 °C. This has been further validated by Hiller (1979), who noted that an increase in post-vernalization (6 weeks) temperature to 27/32 °C (night/day) affected floral stalk elongation in carrots, though the floral differentiation had not been affected adversely. Similar observations were reported by Elballa and Cantliffe (1996), who found an increase in day/night temperature from 17/12 °C to 33/28 °C decreased flower stalk height from 73 cm to 55 cm. This may be due to reduced gibberellic activity at the shoot apex, resulting from warmer temperatures. Despite the photoperiod, the higher temperature (21/17 °C) during the vernalization prevented the formation of reproductive organs in carrots, indicating that the formation of floral organs in carrots is more dependent on temperature than on photoperiods (Samuolienė et al., 2008).

Flowering differentiation has been accelerated by eliminating the far-red light from the illumination at the post-vernalization stage under $21/16 \pm 2$ °C day/night temperature and 16 h photoperiod (Samuolienė et al., 2007). Previous studies indicated that the impact of photoperiod at the post-vernalization stage is minimal in regards to the carrot flowering, the plants could flower at a day length of 9 to 12 hours (Hiller & Kelly, 2019).

Elevated temperature (at 26 °C) has been reported to both increase the number of umbels produced and decrease the number of umbellets per umbel and flower numbers per umbellet (Quagliotti, 1967). Elballa and Cantliffe (1996) have made similar observations on carrot cv 'Hicolor 9' and noted that increasing temperature from 17/12 to 33/28 °C reduced the total number of umbels per plant by 44 %. This is due to the inhibition of growth of lateral branches that hold umbels under high temperature. Furthermore, it has been recorded that the rise of temperature from 14 °C to 26 °C has significantly reduced the ratio of hermaphrodite: male flowers and the fertility of the hermaphrodite flowers as well (Quagliotti, 1967).

Overall, temperature has a greater impact on the floral development of carrot flowers than photoperiod. Furthermore, elevated temperatures during post-vernalization significantly affected the growth and development of floral stalks and reproductive organs in carrots. This leads to fewer umbels and umbellets, which has a direct impact on the quantity and quality of seed production. However, even a smaller number of umbels and umbellets can still produce a higher yield under optimum growing conditions.

2.1.6.4 Pollination and pollinator activities

Abiotic stresses such as high temperature, cold, drought and extreme precipitation can adversely influence the pollination process, altering the growth, development and performance of plant

reproductive parts, flower reward production and foraging activities of pollinators (Descamps et al., 2018; Ramírez & Kallarackal, 2018; Thakur et al., 2010). Previous studies showed that warmer temperature (warmer than the historical average temperature of New Zealand) did not reduce pollen viability (Broussard et al., 2017). However, temperatures above 30 °C during the blooming stage of carrots reduced the receptive period of stigma (Chira et al., 2008). Broussard et al. (2017) suggested that the stigma components attractive to pollinators in carrot flowers such as nectar concentration and volatile emission were affected by higher temperatures. This could affect the foraging behaviour of pollinators subsequently (Broussard et al., 2017). Furthermore, Abrol (2006) observed that the temperatures between 25 and 38 °C positively influenced the attractiveness of pollinators in carrots. However, pollinator attractiveness declined above this temperature range. According to Howlett (2012), the foraging activities of honeybees are higher in warmer conditions (>25 °C) than those of European Blue Blow Fly *Calliphora vicina*, an effective pollinator of hybrid carrots, which is abundant even at 0-10 °C in New Zealand. Moreover, the flower size, diameter, and the sugar concentration of carrots have been significantly affected by environmental factors, especially by temperature, influencing pollinator visitation, fertilization and seed yield (Broussard et al., 2017; Gaffney et al., 2020; Lutfunnahar et al., 2021). Furthermore, it has been noted that adopting controlled irrigation could be beneficial to healthy carrot seed production since the rain at the time of flower development can transmit infections such as bacterial leaf blight and *Alternaria* leaf blight from umbel to umbel via water (Deleuran & Boelt, 2009). Meanwhile, unfavourable thermal and humidity conditions can retard the growth of pollen tubes inside the styles before fertilization (Dyki et al., 2010). The impact of climate change on carrot pollination and pollinators is significant, as time of flowering and fertility of reproductive organs shifts.

Furthermore, the disruption of ecosystems caused by climate change minimizes the activity and efficiency of pollinators. Ultimately, these changes affect carrot seed production.

2.1.6.5 Seed formation and development

Carrot seed development and maturation are also affected by temperature, moisture stress and light intensity (Gray et al., 1988; Hooda et al., 2013). Shading resulted in yield losses in carrot. Carrot seed crops subjected to shading during flowering (3.28 g), 2 weeks before flowering (4.11 g), and 2 weeks after flowering (3.68 g) produced comparatively lower seed weight per plant to non-shaded seed crops (4.42 g) (Gray et al., 1986). This could be a result of reduced crop growth rate as a consequence of reduced intercepted photosynthetically active radiation at flowering (Sandaña & Pinochet, 2011). Most early studies revealed that increments of temperature from 20/10 °C to 30/20 °C significantly reduced the average weight of a single seed. Although the weight of the embryo and endosperm was not affected, the pericarp weight decreased with increasing temperature (Gray et al., 1988). Elballa & Cantliffe (1996), also reported that exposing carrot seed crops at anthesis or before seed development to a warm temperature (33/28 °C) could adversely affect the seed yield and seed quality of carrots. This might be due to the impact of high temperatures, which decrease gibberellin-like activity in the shoot apex, reduce the development of lateral branches, and consequently lead to fewer umbels. The seeds produced at 20/15 °C exhibited comparatively higher progeny vigour (early growth performance of seedlings obtained from the produced seeds as offspring) and germination than seeds formed and developed at 33/28 °C. The importance of optimum irrigation was illustrated by Hooda et al. (2013), and the findings revealed that the carrot seed yield decreased from 10.64 q/ha to 8.06 q/ha when irrigation level moved from 60 mm CPE (cumulative pan evaporation) to 120 mm CPE. The yield reduction suggests that water stress during the reproductive phase can negatively affect seed formation,

development, and overall productivity. In this study, requirement of irrigation was measured based on evaporation (CPE). Deleuran & Boelt (2009) found that cultivating carrot seed crops within tunnels yielded five times higher healthy seed yields than open field conditions. This could be due to tunnel houses enabling controlled drip irrigation systems, thereby keeping the umbels dry and minimizing the transfer of rainwater from umbel to umbel, which can minimize the spread of pathogens.

2.1.7 Crop modelling

2.1.7.1 Types of crop modelling techniques and their pros and cons

Modelling approaches have been widely used as a tool to assess the impact of climate change on crop yield (Hasan & Kumar, 2021; Schmidt & Zinkernagel, 2017). These can be classified as (i) process-based models and (ii) statistical models (Madhukar et al., 2021). Process-based models predict crop yield by simulating the physiological functions of a plant according to climatic factors, soil factors, management practices and endogenous characteristics of plants (Chisanga et al., 2020; Crous-Duran et al., 2019; Stratonovitch et al., 2012). The inclusion of crop physiological mechanisms to determine the impact of weather on crop yield is an advantage of process-based modelling. However, applying process models for predictions of an untested site (actual on-farm conditions) can cause unknown errors. This is due to the use of site-specific experimental data for the validation of the process-based models. Furthermore, factors such as the amount of fertilizer application, pest and disease incidences and weed-controlling methods which are dependent on the behaviour of farmers cannot be accounted for in the process-based models' predictions (Roberts et al., 2017). The inaccessibility of reliable and complete historical data is also one of the constraints in using process-based modelling for climate change projections (Kephe et al., 2021).

In contrast to a process-based model, a statistical model requires only historical weather data and productivity data of a particular crop for climate-crop modelling (Sinnarong et al., 2019).

2.1.7.2. Categories of statistical models

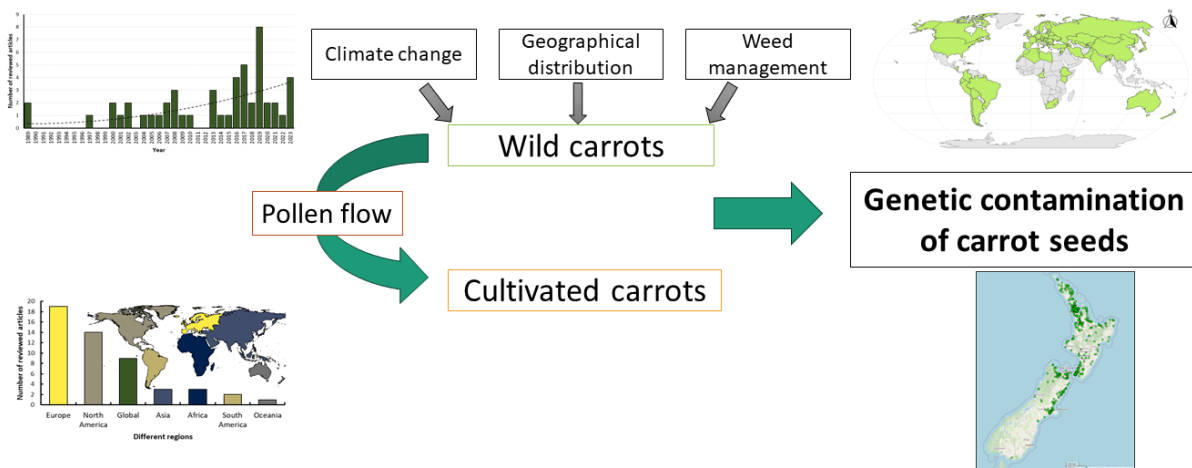
The statistical modelling approach is mainly used to predict the possible impacts of climatic changes on crop yields by using the concept of regression and mathematical equations (Holzkämper et al., 2012; Shi et al., 2013). The statistical modelling approaches can be mainly classified as time series, cross-section and panel methods (Chenu et al., 2017; Dell et al., 2014). The main strength of the panel data approach is the incorporation of time series dimension and cross-sectional dimensions, which yields more precise model estimations than the other two methods (Hsiao, 2011). The presence of individual unobserved heterogeneity could bias model parameters. Thus, the panel data approach can control the unmeasured individual heterogeneity in the model (Lockwood & McCaffrey, 2007).

This review has shown that climate change has an impact on the phenological stages of carrot seed production at every stage. Consequently, it is crucial to plant carrot seed crops in optimal climates for the development of high-quality carrot seeds. However, cultivated carrot fields in temperate and semi-arid regions have been forced to shift from wild carrot-infested locations to avoid genetic contamination which may be climatically less ideal (Broussard et al., 2017). The impact of wild carrots on quality carrot seed production is reviewed in **section 2.2**.

2.2 Pollen-mediated gene flow from wild carrots (*Daucus carota* L. subsp. *carota*) affects the production of commercial carrot seeds (*Daucus carota* L. subsp. *sativus*) internationally and in New Zealand in the context of climate change: A systematic review

This chapter was published in the *Science of The Total Environment* in 2024. Citation: Godwin, A., Pieralli, S., Sofkova-Bobcheva, S., Ward, A., & McGill, C. (2024). Pollen-mediated gene flow from wild carrots (*Daucus carota* L. subsp. *carota*) affects the production of commercial carrot seeds (*Daucus carota* L. subsp. *sativus*) internationally and in New Zealand in the context of climate change: A systematic review. *Science of The Total Environment*, 933, 173269. <https://doi.org/10.1016/j.scitotenv.2024.173269>

Graphical abstract



Highlights

- First systematic review of the impact of wild carrots on carrot seed production.
- From 269 studies, 51 match the requirements to be used in the systematic review.
- Most of the works were conducted in Europe and North America.
- Wild carrots are becoming more adaptable to climate change.
- Wild carrots compromise the genetic purity of cultivated carrots via pollen flow.

Abstract

Climate change will impact the carrot seed industry globally. One adaptation strategy to limit climatic impacts on the production of commercial carrot seeds is geographical shift. However, production must be shifted to climate-optimal places that are free from weeds such as wild carrots to avoid genetic contamination via hybridization. The process of gene flow between wild and cultivated carrots is critical to enable management of wild carrots in the face of climate change. This review systematically assesses the resilience of wild carrots to climate change and their impact on commercial carrot seed production globally with a focus on New Zealand as a major carrot seed producer. The literature was critically analyzed based on three specific components: i) resilience of wild carrots to climate change ii) genetic contamination between wild and cultivated carrots, and iii) management of wild carrots. The majority of the articles were published between 2013 and 2023 (64.71 %), and most of these studies were conducted in Europe (37.26 %) and North America (27.45 %). Country-wise analysis demonstrated that the majority of the studies were carried out in the United States (23.53 %) and the Netherlands (11.77 %). There was limited research conducted in other regions, especially in Oceania (1.96 %). Spatial distribution analysis revealed that the wild carrot was reported in around 100 countries. In New Zealand, the North Island has a higher incidence of wild carrot invasion than the South Island. The findings indicated that the wild carrot is becoming more adaptable to climate change, compromising the genetic purity of cultivated carrots due to pollen flow from wild to cultivated carrots. Therefore, ongoing research will be helpful in developing sustainable weed management strategies and predicting potential geographical invasiveness. This study provides a guide for scientists, policymakers, industrialists, and farmers to control wild carrots and produce genetically pure commercial seeds amid climate change.

Keywords: Cultivar purity; extreme climate; hybridization; invasion; isolation distance; weed management

2.2.1 Introduction

Global climate change impacts are more catastrophic than previously predicted by scientists (Tollefson, 2022). Especially, the sustainability of horticultural crop production is under significant threat due to the predictable and irreversible changes in the atmosphere (Shah et al., 2024). Since crop production is highly sensitive to climate change (Chaudhry & Sidhu, 2022), the supply of agricultural commodities to ensure global food security by meeting the increasing food demand from a growing world population is at risk (Subedi et al., 2023). Furthermore, temperature and rainfall are two extremely important climatic elements that are both affected by climate change and have an influence on crop production (Irwandi et al., 2023). By the end of the century, emissions of greenhouse gases are projected to increase global temperatures between 1.5 °C and 4.8 °C (IPCC, 2023). This will likely affect the water availability for crop production (Waheed et al., 2023). In addition, previous studies stated that as a consequence of climate change, drier areas will have less precipitation in the future, while wetter areas will have more (Konapala et al., 2020; Zeydalinejad & Nassery, 2023).

In New Zealand, climate change resulted in an average two to three-fold increase in the incidence of extreme events and an increase of 1 °C mean temperature (Thomas et al., 2023). Moreover, rainfall patterns in New Zealand are projected to change, with the North Island and the east of the South Island, which includes major carrot seed-producing areas, becoming drier. As a result of changes in the temperature and rainfall, both the severity and the frequency of summer droughts

are expected to rise in the coming decades (Mullan et al., 2018). These facts make it apparent that both internationally and in New Zealand, climate change is a major issue for seed production.

In 1850, the New Zealand seed industry started with the cultivation of *Dactylis glomerata* L. Since then, New Zealand has become one of the leading seed producers, processors, and exporters of an extensive variety of horticultural, arable and pastoral crops across the globe (Chynoweth et al., 2015; Robertson & Hurren, 2019). The high quality of New Zealand seed is critical to the sector's international success and is maintained due to the adoption of appropriate technologies in plant breeding for the development of high-yielding varieties, with verification of variety through the production system (New Zealand Seed Certification scheme) and/or strict production quality control within seed companies combined with verification of the quality of the seed produced (International Seed Testing Association- accredited laboratories). Meanwhile, private sector bodies such as the Foundation for Arable Research (FAR) and Seed Industry Research Centre (SIRC) invest considerable funding in research and development programmes to enhance the quality of seed production (Rubenstein et al., 2021). These strategies have boosted seed production and ultimately export earnings. As a result, over the past 5 years, the export value of fruits, vegetable, tree, and flower seeds has increased by almost 15 % (2023: \$106.15 million and 2019: \$ 90.2 million). This was due predominantly to the increased demand for the seeds of carrots and radishes produced in New Zealand (FreshFacts, 2023).

Carrot seed production has expanded globally in response to the growing demand for high-quality planting materials, driven by a rising world population (Chandra et al., 2022; Moore et al., 2021). New Zealand (Southern Hemisphere) and Central Oregon (Northern Hemisphere) are the world's top producers of hybrid carrot seeds, accounting for 50 % and 40 % of the global market, respectively (Moore et al., 2021; Preece, 2023).

The phenological phases of carrot seed crops and their pollination process are extremely sensitive to changes in climatic factors (Godwin et al., 2023), meaning that the carrot seed industry is likely to be also severely affected by climate change. One adaptation approach is the geographical shift of carrot seed production. However, other factors that will negatively impact carrot seed production, such as weed contaminants, must be factored in when considering climate-optimal locations. Wild carrot (*Daucus carota* L. subsp. *carota*, one of the most common wild carrot species around the world, including New Zealand) has significant potential genetic contaminations via hybridization. Already the production location for cultivated carrots in temperate and semi-arid regions has been forced to shift from wild carrot-infested locations to others that may be climatically less ideal (Broussard et al., 2017), confirming that wild carrot already generates a serious problem for production of quality carrot seeds in an era of global climate change.

Wild carrot, commonly referred to as Queen Anne's lace, is a close relative of cultivated carrots, and both belong to the family Apiaceae (Iorizzo et al., 2013; Rong et al., 2010). Due to its invasive nature, wild carrot is considered a serious weed in some countries such as the USA, Afghanistan, Hungary, Poland, and Greece (Kumarasamy et al., 2005; Van Etten & Brunet, 2017). The sexual compatibility of wild and cultivated carrots permits spontaneous hybridization, and cultivar purity in commercial seed lines can be compromised due to gene flow from wild to cultivated carrots (Hernández et al., 2023). The presence of genetically impure carrot seeds is not accepted by seed merchants. Carrots of poor genetic quality will affect the reputation of the nations that produce carrot seeds (Magnussen & Hauser, 2007). Hence, it is important to control the wild carrots prior to the flowering phase to stop the undesirable gene flow. Furthermore, wild carrots can be hard to control after they flower due to their deep taproots and prolific seed formation. Wild carrot seeds can remain dormant from a year to seven years before germination. As a result, a seed bank of

wild carrots can be easily created in the soil profile, which can make eradication more challenging (Dale & Harrison, 1966; Magnussen & Hauser, 2007). Meanwhile, wild carrots can produce a 5 - 50 cm deep taproot, which facilitates stocking energy for the consequent regrowth and creates difficulties for removal (Hilty, 2015; Praciak, 2015). Due to its adaptability to a wide range of soil conditions, wild carrots may also thrive in sandy or gravelly soil (Colquhoun et al., 2003).

Climate change is predicted to result in changes in the composition of weed communities, growth dynamics, life cycle, phenology, and degree of infestation (Anwar et al., 2021). Most previous studies on how climate change affects wild carrots have focused on selecting suitable genotypes of carrots, including wild carrots, which suggests that scientists tend to concentrate on the breeding perspective in order to better respond to future climate change (Bolton et al., 2019; Mezghani et al., 2019; Simon et al., 2021). However, it is crucial to investigate how wild carrots survive and expand under climate change conditions. Making recommendations on where to establish carrot seed crops also relies extensively on knowing the geographical distribution of wild carrots in the context of regional and global scales. In the context of carrot breeding, most of the previous investigations primarily studied how introgression (pollen flow) from cultivated to wild carrots has an impact on the survival of the hybrids and their evolution in the natural habitat as aggressive weeds (Magnussen & Hauser, 2007; Mandel et al., 2016). This is due to the main concern on the escape of beneficial alleles (transgene escape) from cultivated to wild carrots (Hernández et al., 2023). From the perspective of carrot seed producers and seed industries, it is essential to understand how pollen-mediated gene flow from wild to cultivated carrots affects the global and regional production of commercial carrot seeds in the face of climate change.

A review of existing literature on the resilience of wild carrots to extreme climatic conditions and their implications on the cultivar purity of cultivated carrots has been lacking until now. Therefore,

we present, to the best of the authors' knowledge, the first systematic review at the national and regional levels, recognizing the significance of the impacts of pollen flow from wild to cultivated carrots on commercial carrot seed production. New Zealand was selected for the regional scale study due to its position as a significant producer of carrot seeds in the Southern Hemisphere. The current review aimed to investigate and summarize how pollen-mediated gene flow from wild carrots to cultivated carrots affects the quality of the cultivar purity, especially at global and regional (New Zealand) scale, based on studies conducted recently. To address this aim, we formulated three different research questions:

- (1) To what extent do wild carrots exhibit resilience to extreme climatic conditions?
- (2) How does pollen-mediated gene flow from wild to cultivated carrots affect the cultivar purity of the commercially produced carrot seed?
- (3) What are the strategies that can be adopted to control the pollen flow from wild carrot plants to adjacent carrot seed crops when they flower synchronously?

This review will provide a reference for the scientists, policymakers, industrialists, and farmers who are involved in carrot seed production to control wild carrots and produce genetically pure commercial seeds amid climate change. Moreover, the highlights of this study can serve as a pathway to fill the research gaps via future research in the context of quality carrot seed production.

2.2.2 Material and methods

2.2.2.1 Literature search and data collection

This systematic review was conducted using six steps (1. Scoping, 2. Planning, 3. Identification and search process, 4. Screening articles, 5. Eligibility assessment and, 6. Interpretation and

presentation) as suggested by Koutsos et al. (2019). As the first step (1. Scoping), the procedure for the systematic review was established. Consequently, the PRISMA (Preferred Reporting Items for Systematic Reviews and Meta-Analyses) protocol was selected to ensure the scientific quality of the review (Liberati et al., 2009). Finding appropriate databases was the second step (2. Planning) in the systematic literature review. To guarantee the selection of rigorous peer-reviewed articles, an extensive search of the literature was carried out using the SCOPUS and PubMed online databases. Two distinct search words connected by the “AND” and “OR” connectors were used to carry out basic searches. Precisely, the literature search was conducted using the following keywords: Carrot* AND “wild relative*” OR “wild carrot*” OR “carrot wild*” OR “queen anne’s lace*” AND distribut* OR stress* OR toleran* OR adapt* OR resilience* OR resista* OR climat* OR pollen* OR gene* OR “Isolation distance” OR “outcross*” OR control* OR management*. For the third step (3. Identification and search), articles were identified from SCOPUS and PubMed databases through to the end of 2023. The initial literature search was performed on the 29th of January 2024 and resulted in 204 search returns after excluding the duplicate articles. Publications were screened in the 4th step to determine if their titles and abstracts aligned with the review’s research questions. In addition, articles that are not in the English language and review articles or book chapters were excluded from this systematic review. Eligibility of the Full-text articles was checked in the 5th step and those that failed to address the research questions were excluded. Overall, 51 articles were determined to be eligible for the systematic review. Following a comprehensive investigation, the selected articles were categorized into three different research topics: Resilience of wild carrots under climate change, genetic contamination between wild and cultivated carrots, and management of wild carrots. As the 6th step (interpretation and presentation), selected articles were summarized and discussions were constructed to answer the

research question. The review process and the number of articles in each review stage are shown in **Figure 2.5**. Only one peer-reviewed article from New Zealand was found during the literature search. Therefore, several grey literatures (e.g., dissertation) articles were included in the review after a manual search from Google Scholar (See et al., 2023).

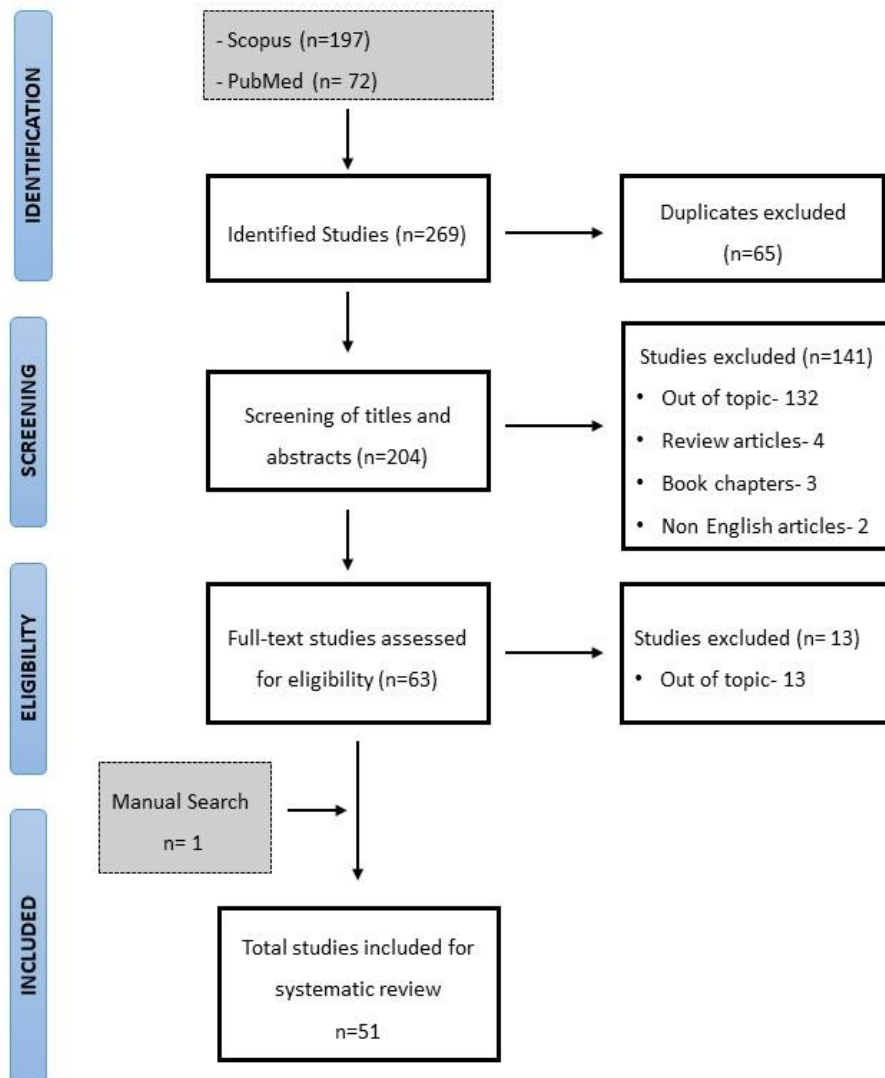


Figure 2.5 Flow diagram for review process and selection of articles

2.2.2.2 Data collection to map the spatial distribution of wild carrot

The distribution of wild carrots in New Zealand could not be determined by using previous literature due to a lack of data, consequently, iNaturalist NZ, one of the most significant sources of spatial information on the global distribution of different species, was used to identify the distribution pattern (Contreras-Díaz et al., 2023). All the research-grade (verified by at least two members of iNaturalist NZ) wild carrot observations ($n = 709$) were downloaded from iNaturalist NZ on the 28th of August 2023 and the latitude and longitude were extracted to map the distribution of wild carrots, consequently (Rogers & Clarkson, 2023). The shape files for the development of maps were downloaded from Stats NZ Geographic Data Service (NZ Stats, 2023). The spatial maps were generated by using Rstudio (version 2022.07.2 + 576), whereas the graphs were created by using Microsoft Excel.

2.2.3 Results and discussion

2.2.3.1 Historical and spatial context of the selected articles

The number of reviewed articles ($n= 51$) distributed by year of publication is illustrated in **Figure 2.6**. Over the period, it is evident that the number of articles about wild carrots, especially in the context of their distribution, resilience to climate change, gene flow, and management, has shown an increasing trend. Overall, approximately 64.71 % of the articles were published between 2013 and 2023. Notably, there were 8 articles published in 2019 alone. Nevertheless, only 9 articles were published between 2020 and 2023 relevant to these study questions. This might be due to the lack of research activities and international collaborations as a result of the COVID-19 pandemic. The primary reasons for the increase in the publication in the past few decades are the growing recognition of the impact of climate change on carrot production and the prospective introduction

of transgenic (or genetically modified) carrots. As a result, breeders and scientists wanted to understand how wild relatives of carrots adapt to climate change and how to use those wild genotypes to strengthen the carrot breeding to withstand the abiotic stresses, as well as to research the possibility of transgene introgression from GM carrots into their wild relatives.

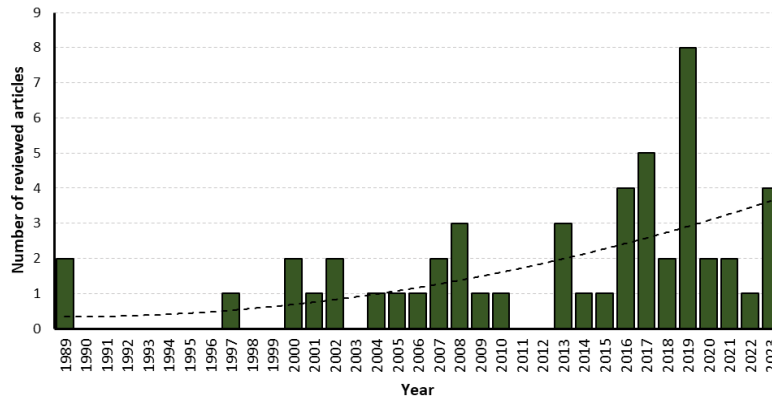


Figure 2.6 Number of reviewed articles (n= 51) published by year

The continent-based spatial distribution of the reviewed articles is shown in **Figure 2.7A**. The results of this literature search showed wild carrots have spread globally except to the region of Antarctica. European colonization and the importation of contaminated cultivar carrot seeds with hybrids (wild × cultivated) are the important causes for the introduction of wild carrots to new geographical locations (Iorizzo et al., 2013; Magnussen & Hauser, 2007). Furthermore, the majority of research on the distribution, gene flow, management and survival of wild carrots has been undertaken in Europe (19) and North America (14), which are the two main regions for the production of carrot seeds in the Northern Hemisphere. This finding indicated the importance of understanding the behaviour and spatial distribution of wild carrots particularly in carrot seed-producing regions. Comparatively, there are fewer studies on wild carrots, particularly those related to climate change and gene flow, in areas like Asia (3), Africa (3), South America (2), and Oceania (1). Furthermore, 9 articles focused on the global scale. In comparison to other continents, relatively little research has been done on wild carrots in Oceania (Australia and New Zealand).

Most of the 51 studies were conducted in a small number of countries (**Figure 2.7B**): 23.53 % were conducted in the United States (n=12), 11.77 % in the Netherlands (n=6), and 9.8 % in Denmark (n=5). However, research efforts were observed in other countries as well. i.e., Tunisia (3 papers, 5.88 %), Canada, Portugal and Argentina (2 papers, 3.92 % each), and India, Syria, New Zealand, Macaronesian Islands and Scotland (1 paper, 1.96 % each).

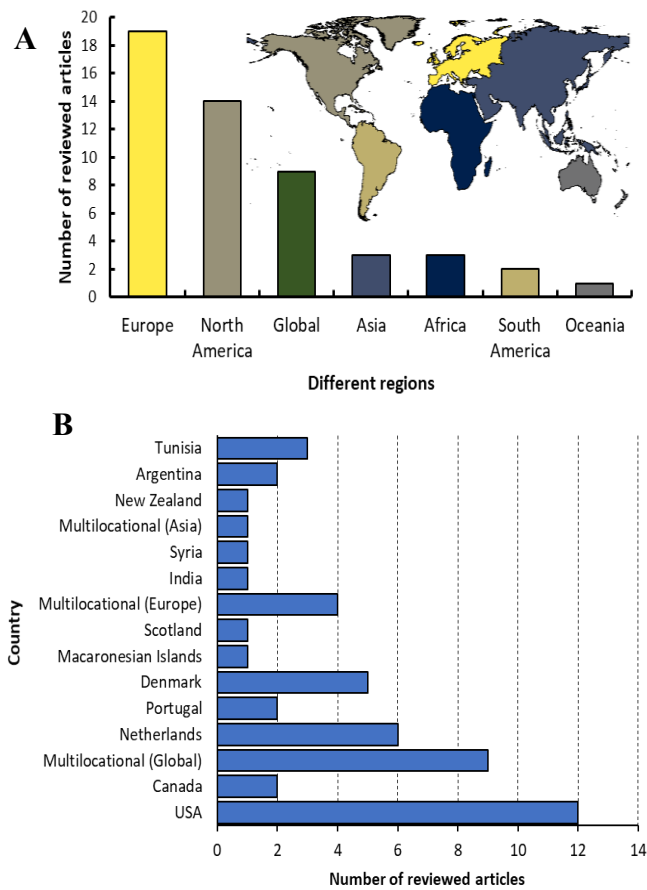


Figure 2.7 Geographical coverage of reviewed articles (n=51); **A**, based on continents and **B**, based on countries

2.2.3.2 Wild carrots and their effect on quality carrot seed production

2.2.3.2.1 Resilience of wild carrots under stressing climatic conditions

The ability of wild carrots to adapt to changing climate conditions is an important factor in the gene flow from wild to cultivated carrots. Wild carrot is an invasive weed (de Jong et al., 2016; Palmieri et al., 2019), that shows a wide range of variations in the context of germination, vegetative, and reproductive growth phases to abiotic stresses, such as heat, drought, and salinity (Simon et al., 2021). In terms of seed germination, a number of wild carrot accessions have shown significantly less germination percentages than the cultivated carrots under heat (35 °C), drought (-0.58 MPa), and salinity (150 mM NaCl) stress conditions, due to climate change. However, there were significant differences between wild carrot accessions from various geographical regions. For example, seeds of wild carrots from Pakistan, Portugal, Tunisia, and Turkey were found to be heat tolerant during germination. Whereas wild carrot seeds from Pakistan and Turkey showed evidence of tolerance to salinity during germination (Bolton et al., 2019; Bolton & Simon, 2019; Mezghani et al., 2019; Nijabat et al., 2023). In addition, compared with existing commercial carrot cultivars, such as the salt-tolerant cultivar "CAS," wild carrots were shown to have more germinability at higher salt concentrations (300 mM NaCl), indicating the resilience of wild carrots (England 79686^a) to the increased extreme saline conditions. Wild carrots found in a coastal environment (England 79686^a) performed better under saline conditions than the wild carrots inland (Azerbaijan 769446^a), suggesting that the adaptability to the saline environment may depend on the provenance (location) of the wild carrot (Bickler et al., 2019).

^a The numerical value next to the country represents the seed bank accession number of *Daucus carota*

The degree of heat tolerance of wild and cultivated carrot seedlings was compared by Nijabat et al. (2020), who found that the wild carrot was significantly more susceptible to cell membrane injuries during the early and late seedling stages caused by extreme (35 ± 3 °C) heat exposure. Meanwhile, cell membrane stability at the seedling stage also significantly differed among the wild carrot accessions originating from different countries (Nijabat et al., 2020). In cultivated and wild carrots, the *DcAOXI* gene has proven to be particularly reactive to stress stimuli caused by environmental changes (Nogales et al., 2016). As a result, Nobre et al. (2016) utilized *DcAOXI* to identify the hotspots of carrot crop wild relatives (CWR) across Europe. They found variation in *DcAOXI* in populations of wild carrots sampled under different environmental conditions in West-Europe, which suggested varying levels of climatic adaptation in different populations. These findings were further validated by Cardoso et al. (2017), who found high variability in *DcAOXI* across the carrot wild genotypes collected from three different climatic regions, (hot summer Mediterranean climate, hot summer continental climate, and humid subtropical climate).

According to the geographical distribution, wild carrots, especially in the regions of France, Sweden, and Portugal, have exhibited significant variation in leaf growth, flowering phenology, and number of umbels at harvest, which emphasises how wild carrots respond themselves to various environmental conditions (Geoffriau et al., 2019). Furthermore, Simon et al. (2021) reported that the carrot CWR from the regions of northern Africa, central Asia, and Anatolia have a notable level of resilience to abiotic stressors. According to Mezghani et al. (2019), certain endemic wild carrot species (*Daucus syrticus* and *Daucus carota* subsp. *capillifolius*) have shown signs of potential adaptability to high temperatures and minimal rainfall in parts of Tunisia and neighbouring Libya. Camadro et al. (2008), similarly reported that *Daucus pusillus* showed tolerance to the adverse abiotic factors in the Argentinian region due to its adaptable nature to the

extensive range of macro environments including dry, cold, humid, and warm climatic conditions. Furthermore, wild carrot species have been shown to survive in Syria in a variety of climatic conditions with respect to the different ranges of altitude (sea level – 1800 m) and precipitation (350 – 1000 mm). However, places with an annual precipitation of over 500 mm observed a larger distribution of wild carrots (Al-Safadi, 2008). According to Hauser (2002), wild carrots have a higher chance of surviving frost stress than cultivated carrots and their hybrids (wild × cultivated). The fact that wild carrots required a shorter period (5-30 days) of cold temperatures (5 °C) to induce flowering highlights their ability to begin flowering with minimal vernalization-an important strategy for producing large quantities of seeds before severe winter conditions (Wohlfeiler et al., 2019). Moreover, Van Etten & Brunet (2014) stated that the rising trend in winter temperatures caused by global warming could improve overwinter survival and the proliferation of wild carrots. The capacity of wild carrots to withstand abiotic stress has been further demonstrated by Simon et al. (2021), who suggested that abiotic stress tolerances found in the CWR gene pool can be transferred into cultivars via carrot breeding programs. All of these findings imply the importance of studying the relationships between the survival of wild carrots and abiotic stresses seen at the various eco-geographical locations. Meanwhile, it's essential to conserve the genetic resources of wild relatives for future breeding efforts since many populations that provide the genetic diversity of wild carrots are endangered as a result of changing climatic circumstances (Mezghani et al., 2019).

Finally, it is evident that the resilience of wild carrots under changing climatic conditions can differ depending on the environmental factors and genetic structure and composition of the plant. Although wild carrots have adapted to survive in a wide range of environments, it is vital to remember that their resilience may have limitations and that they may still face difficulties

surviving in extremely harsh or changing climates. Moreover, prolonged climate change might affect the dynamics of the natural habitats, which can impact the overall capacity for survival in adverse climatic conditions. Meanwhile, wild carrots can thrive close to the locations where carrot seeds are produced, as both cultivated and wild carrots depend on favourable climatic conditions. Consequently, when shifting a carrot seed production paddock to a place with optimum climatic conditions to overcome issues related to climate change, cultivar purity of the commercial carrot seed can be threatened through genetical contamination if wild carrots exist and flower within the isolation distance of cultivated carrot seed crops.

2.2.3.2.2 Genetical contamination between wild and cultivated carrots

The characteristics of wild carrots and their impacts on gene flow and commercial carrot seed production are summarized in **Table 2.1**. Wild and cultivated carrots belong to the same family. Consequently, it is quite challenging to distinguish between their populations prior to the reproductive phase (Mezghani et al., 2017). Furthermore, wild carrots can exhibit various life history strategies, including winter annual, summer annual, biennial, and monocarpic perennial, which mainly rely on genetics and environmental factors (Van Etten & Brunet, 2017). As a result, the time and pattern of flowering vary across different geographical locations (de Jong et al., 2016; Wohlfeiler et al., 2019). The presence of populations of wild carrots with an annual behaviour is more advantageous for gene transfer (as pollen or seeds) than biennials and perennials due to the higher number of flowering wild carrots expected from the annual wild carrots within a year. The degree of spontaneous hybridization between wild and cultivated carrots is anticipated to be high since the carrot is a cross-pollinating species with a large diversity of pollinators (Koul et al., 1989; Nobre et al., 2017; Roxo et al., 2021). Previous studies indicated that the carrot gene flow from wild to cultivated is higher than from cultivated to wild, despite the fact that gene flow is

bidirectional (Rong et al., 2014). This is further clarified by Rong et al. (2010), who noted that the high outcrossing incidence (approximately 96 %) in wild carrots results in a substantial frequency of pollen exchange among the carrot subspecies. One of the traits of wild carrots that assists with pollen dispersal is long-lasting pollen viability (up to 10 days). Ibañez & Camadro (2015) reported that the wild carrot accessions in Argentina have high pollen viability of over 87 %. Climate change may also have a significant effect on pollinator activities. Due to the higher pollen viability rate of wild carrots compared with cultivated carrots, the required pollen deposition of wild carrot pollen on receptive cultivated carrots is lower, and consequently, pollination can be attained with fewer insect visitations (Broussard et al., 2017). Moreover, wild carrots and their hybrids (wild × cultivated) have been observed adjacent to commercial carrot production sites in places all around the world (Ellison et al., 2018; Magnussen & Hauser, 2007), which can significantly affect the genetic purity of the commercial carrot seeds via undesirable pollen transfer from wild to cultivated carrots when both flowers simultaneously (Hauser & Bjørn, 2001; Hauser & Shim, 2007; Rong et al., 2010). Due to this, carrot seed production is generally carried out in an area free of wild carrots (Hernández et al., 2023; Rong et al., 2013).

Maintaining a high percentage of genetic purity is an essential criterion for successive multiplications and supplying quality carrot seeds to the global seed market. Rong et al. (2010) emphasised the need to maintain genetic purity by stating that hybrid carrot seeds from wild and cultivated carrots (wild × cultivated) should make up less than 0.005 % of the overall carrot seed lot. Similar requirements apply in New Zealand, where the minimum cultivar purity level has to be maintained at around 99.98 % for the export market (Bhatia, 2023). When the percentage of contaminated seed exceeds the acceptable level, seed lots may be discarded (Magnussen & Hauser, 2007). The presence of bolters, which is a type of hybrid (wild × cultivated) flowers in their first

year, in the carrot taproot production sites is a consequence of using impure carrot seed lots since the early flowering is a dominant nature of the wild carrots (Schönegger et al., 2022; Wijnheijmer et al., 1989). Consequently, these bolters can hybridize with the wild carrots present in the adjacent area and enhance their population in the carrot production sites (Hauser & Bjørn, 2001; Hauser & Shim, 2007). Wild carrot roots are white since they do not acquire carotenoid pigments, whereas the roots of cultivated carrots accumulate significant levels of carotenoids, giving them their distinctive orange colour (Just et al., 2009). Comparatively, the wild carrot's root is typically smaller and fibrous in structure than the cultivated carrots (Grebenstein et al., 2013; Shim & Jørgensen, 2000). In terms of root traits including colour, shape, and flavour, roots established from contaminated seeds (wild × cultivated) have also demonstrated similarities to intermediate characteristics of wild and cultivated carrots, though these roots are inedible and nonmarketable (Magnussen & Hauser, 2007; Wijnheijmer et al., 1989). Furthermore, the exportation of these contaminated seeds along with the commercial carrot seed lots to other farming regions may result in the introduction of wild carrots in new geographical areas (Bradeen et al., 2002; Hauser & Shim, 2007). Due to this, breeders and seed producers attempt to avoid pollen flow from wild to cultivated carrots (Mandel et al., 2016; Shim & Jørgensen, 2000).

Overall, it is clear that the existence of wild carrots adjacent to the commercial carrot seed-producing field can negatively affect the quality of the commercial seed lots. Due to the pollen transfer from wild to cultivated carrots, undesirable characteristics, such as white root and bitterness of wild carrots can be transmitted to commercial carrots, which can result in genetic variability and problems in maintaining the beneficial traits of commercial carrots. When it comes to the appearance, flavour, and quality of carrots, customers and agricultural stakeholders have certain expectations. The introduction of undesirable characteristics to commercial carrots via

pollen flow from wild carrots can lead to seeds that produce carrots that fail to reach quality standards. Consequently, seed producers face difficulties in promoting their products and sustaining customer satisfaction.

2.2.3.2.3 Spatial distribution of wild carrots

2.2.3.2.3.1 Global context

Wild carrots are native to western Asia and Europe (Rong et al., 2010), even though they have since become widespread as an invasive weed all around the world via human activities, such as agriculture, settlement, and trade as well as through natural processes (seed dispersal via animals and wind) (**Figure 2.8**). In addition, climate change also can increase the spatial distribution of wild carrots by varying the habitat suitable for their survival. Due to their wide adaptability and prolific seed production, wild carrots can quickly establish and spread once they are introduced to a new geographical location. The findings of this study indicated that the wild carrot has now invaded around 100 countries. Among them, wild carrots have also spread to the main carrot seed-producing regions, including the United States, and New Zealand, threatening the production of genetically pure carrot seeds (Iorizzo et al., 2013; Rong et al., 2010). In addition, the results of this review confirmed that wild carrots are densely populated in temperate climatic regions due to their adaptive nature (Hernández et al., 2023). Based on the geographical distribution of wild carrots (**Figure 2.8**), it is clear that this weed is less common in African and Southeast Asian regions compared with other regions. The climatic barriers, such as tropical climate, and geographic features could all be factors limiting the invasion of wild carrots in these regions.

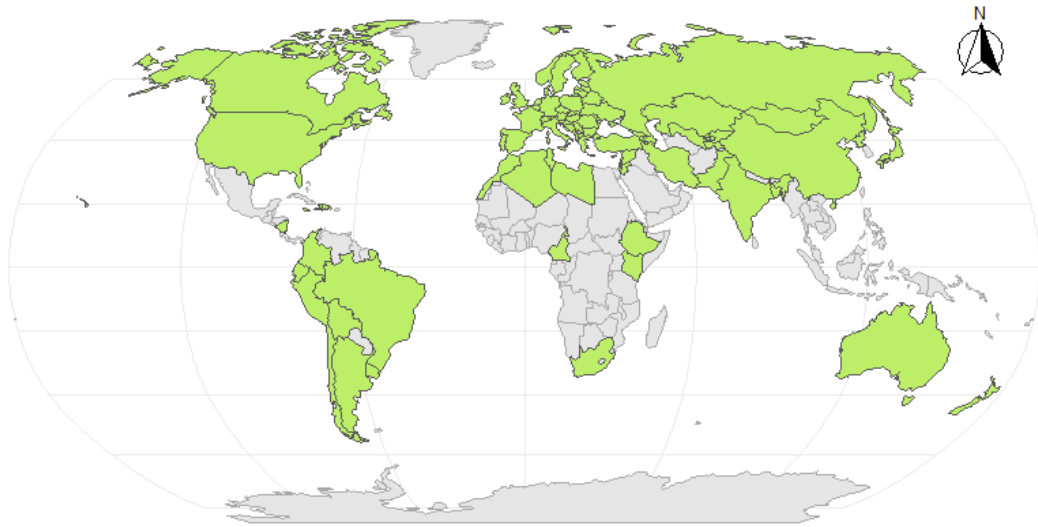


Figure 2.8 Map demonstrating the global wild carrot distribution based on reviewed articles (n=51) and data collected from iNaturalist

2.2.3.2.3.2 New Zealand

New Zealand is one of the major carrot seed producers in the global market (Bhatia, 2023). Due to seasonal variations, carrot seed production is possible in New Zealand. Cool winter temperature is an essential requirement to induce the flowering of carrots, which is easily achieved in New Zealand during the months of June and July (Wohlfeiler et al., 2019). The production of carrot seeds is primarily based in the Canterbury and Hawke’s Bay regions in New Zealand. However, wild carrots are widely distributed throughout New Zealand (Kumar et al., 2023) except for the Southland. It is also evident that the North Island of New Zealand has experienced a more severe invasion of wild carrots than the South Island (**Figure 2.9**). In comparison with the South Island, the North Island generally experiences warmer and wetter climate, as well as significant levels of human-induced habitat changes. These conditions could favour the proliferation and growth of wild carrots, making it possible for them to invade more vigorously the North Island than the South

Island of New Zealand. Furthermore, the presence of the wild carrot hotspots in Hawke’s Bay and Canterbury regions can be a critical threat to the quality carrot seed production in New Zealand (Bhatia 2023). These facts make abundantly evident how critical it is to keep the breeding stock and seed lots pure by controlling the wild carrots around farms used to produce quality carrot seed (Hauser & Bjørn, 2001). The goal of management efforts is to reduce wild carrots’ impact and restrict their spread by using a combination of chemical, mechanical, and training approaches. The management of this invasive species is a current challenge, which requires collaboration between conservation organizations, government agencies, and the public. **Figure 2.9** is not a complete survey map of wild carrots, but rather a visual representation created based on different observations from photographers and naturalists.

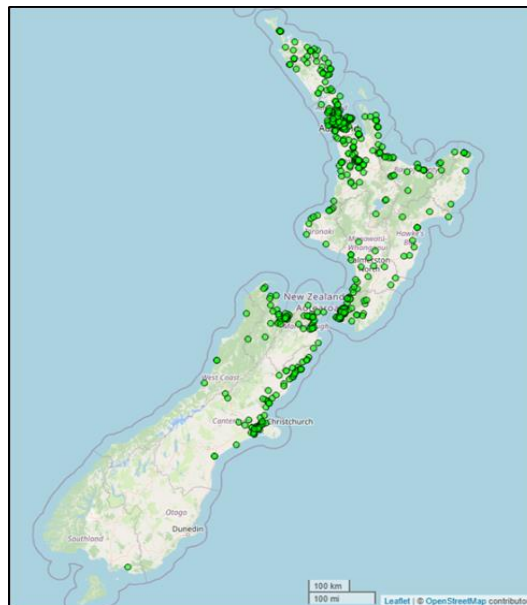


Figure 2.9 Wild carrot invaded locations in New Zealand
(OpenStreetMap contributors, 2017)

2.2.3.2.4 Strategies used to minimize pollen flow between wild and cultivated carrots

Wild carrots must be controlled before flowering in order to minimize their proliferation and long-distance pollen flow to the adjacent flowering carrot seed crops (Rong et al., 2010, 2013). Therefore, the weed management strategies ought to focus primarily on reducing the flowering rate and the overwinter survival of wild carrots. Moreover, allowing one wild carrot to produce seeds might hypothetically result in a population growth of 382 individuals in just three years (Van Etten & Brunet, 2017). Similarly, it has been reported that, between 1994 and 2003, wild carrot infestation in Western Oregon doubled in severity and expanded spatially (Mueller-Warrant et al., 2008). This clearly indicates the need for timely management of wild carrots to minimize their severity and invasiveness.

Previous research revealed that tilling the area around the seed carrot crop field is a successful mechanical weed management strategy for controlling the wild carrot population (Stachler & Kells, 1997). Rong et al. (2013) expanded that the most effective approach for managing wild carrots is to pull or mow the wild carrot plants closer to the ground at or just before flowering. Wild carrots may become invasive as a result of being mowed when mature seeds are present. This is particularly due to the gene flow via the dispersal of seeds. Therefore, it's critical to comprehend the phenological stage of the wild carrot population before mowing. Meanwhile, Rome & Lucero (2019) have observed that the removal of entire plants is the most efficient method to lower the number of existing wild carrots than the hand removal of seed heads and clipping at base height. Moreover, Mueller-Warrant et al. (2008) highlighted the primary reasons for the proliferation of wild carrots include changes to the planting method and a decrease in crop rotation, particularly with cereals. Crop rotation, especially when using fall-planted cereals like wheat, can effectively control infestations of wild carrots since wheat is usually harvested while wild carrot is still

flowering. This prevents seed production and decreases the number of overwintering plants in subsequent seasons.

The fact that wild carrot pollen can disperse up to 4.2 km via pollinators highlights the need for longer isolation distances (Rong et al., 2010; Roxo et al., 2021). However, pollen-mediated gene flow is primarily based on pollen viability, pollinator behaviour, and environmental factors, making the necessity for isolation distance regionally dependent. For instance, in order to prevent their crops from crossing with wild carrots, farmers who grow carrot seeds frequently maintain an isolation distance of 3 km in the Netherlands (Rong et al., 2010) and 2 km in New Zealand (Bhatia, 2023). Growing carrot seed crops in the midst of mountain ranges, as long as there are no wild carrots present in the mountain ranges, can be used as a strategy to naturally restrict pollen movement (Ellison et al., 2018). This approach is not practicable for the large-scale seed producers, though it could be used by small-scale seed producers around the world, such as in Uttarakhand, India. Furthermore, to maintain pollen flow between cultivars below a specific threshold, a cultivated carrot field with a higher density of flowers and/or a wild carrot population with a lower density may require a much longer isolation distance (Rong et al., 2010). Therefore, it is crucial to scout for the existence of wild carrots at the location where carrot seeds are produced, considering the isolation distance. However, this requires a lot of work and time. The potential of airborne hyperspectral remote sensing to quickly and accurately identify plant species at large spatial scales has been demonstrated by Bhatia (2023), who has used this technology to locate wild carrot plants within the isolation distance of the carrot seed crops.

As shown in **Table 2.2**, the application of a chemical spray is also an effective tool that can be used to control wild carrots. However, chemical control of wild carrots in commercial carrot seed production has not been studied previously. In the context of organic management of wild carrots,

Lefebvre et al. (2018) examined the effectiveness of applying Indian mustard as a biofumigant and observed 95% mortality during seed germination of wild carrots. Similarly, Hill et al. (2006) noted that the application of cowpea (*Vigna unguiculata* (L.) Walp) and hairy vetch (*Vicia villosa* Roth) aqueous extracts in concentrations of 0.00-8.00 gL⁻¹ has rapidly controlled the growth of wild carrots under laboratory conditions via inhibiting the radicle elongation. As far as herbicides are concerned, post-emergence applications aimed at managing wild carrots may injure carrot seed crops as well, since both wild and cultivated carrots are members of the same species. Consequently, it is necessary to determine if there are herbicide combinations and dosages for controlling wild carrots without injuring the carrot seed crops. In addition, the time of application is also an important phenomenon in controlling wild carrots. Herbicide is most effective when sprayed late in the fall and/or early in the winter to maximize the mortality of overwintered wild carrots prior to the initiation of the reproductive phase (Van Etten & Brunet, 2017). Furthermore, Stachler & Kells (1997) stated that plant size and environmental conditions are the main factors in the susceptibility of wild carrots to herbicides such as glyphosate. Due to this, the herbicide recommendations including the type and rate varied according to the growth stages of wild carrots (**Table 2.2**). Conversely, Stachler et al. (2000) found that 69 % of the tested wild carrot plants have exhibited resistance to the 2,4-D in the Canadian region, which is predominantly due to the extensive usage of 2,4-D since the late 1940s. This makes it evident that regular changes are necessary when spraying herbicides to manage wild carrots. Based on the available chemistry, it is possible to use different herbicides with various modes of action to control wild carrots (outside of commercial carrot seed production sites), thereby preventing the selection pressure for resistance to a particular herbicide (**Table 2.2**).

Climate change creates additional challenges in controlling wild carrots. Particularly, changing climatic conditions can create more beneficial conditions for wild carrots to enhance their invasiveness. Furthermore, increasing trends of temperature, variations in rainfall patterns, and seasonal changes could enhance the wild carrot's adaptability, requiring proactive steps to manage and control their spread to new locations. Therefore, the management strategies also need to be updated according to the evolving nature of the wild carrot's phenology, invasiveness and adaptability to climate change. Overall, it is evident that adaptive and dynamic strategies are needed to control wild carrots in the face of climate change.

Table 2.1 Summary of wild carrot characteristics and their impacts on gene flow and commercial carrot seed production

Features of wild carrots	Impact on gene flow (wild to cultivated carrots)	Reference
Wild and cultivated carrots are sexually compatible	Facilitates cross-pollination between wild and cultivated carrots	Hauser & Bjørn (2001); Hauser (2002)
Surviving close proximity to the carrot seed crops	Facilitates pollen transfer from wild to cultivated carrots	Ellison et al. (2018); Magnussen & Hauser (2007)
Existence of various life history strategies (winter annual, summer annual, biennial, and monocarpic perennial)	Higher probability of overlapping the flowering periods with cultivated carrots	Van Etten & Brunet (2017)
Ability to attract a large diversity of pollinators	Higher degree of spontaneous hybridization with cultivated carrots	Koul et al. (1989); Nobre et al. (2017); Roxo et al. (2021)
Exhibiting a high outcrossing percentage (approximately 96 %)	Facilitates higher frequency of pollen transfer between wild and cultivated carrots	Rong et al. (2010)
Long-lasting (> 10 days) and high pollen viability (> 87 %)	Increases the success rates of pollination and fertilization between wild and cultivated carrots	Ibañez & Camadro (2015)

Table 2.2 Recommended herbicides for management of wild carrots based on previous research findings

Growth stage of wild carrot	Common name of herbicide	Recommended rate of application	Targeted Crop production	Reference		
Pre-Emergence	Acetochlor + dichlormid	1793 + 309 g ai/ha	-	Stachler & Kells (1997)		
	Cyanazine	3026 g ai/ha				
	Germination	Linuron + Chlorimuron			557 + 31 g ai/ha	
	OR	Metribuzin + Chlorimuron			336 + 32 g ai/ha	
	early	Atrazine + mesotrione + S-metolachlor			561 + 150 + 1,504 g ai/ha	
	emergence	Atrazine + mesotrione + S-metolachlor			1,122 + 300 + 3,008 g ai/ha	Canaan fir
	Hexazinone + sulfometuron methyl	289 + 27 g ai/ha			- POST	Aulakh (2020)
Post-Emergence	Hexazinone + sulfometuron methyl	480 + 46 g ai/ha				
	Bentazon	1121 g ai/ha		Stachler & Kells (1997)		
	Seedling	Cyanazine	2212 g ai/ha			
	Picloram + 2,4-D	0.23 + 0.84 kg ai/ha	Orchardgrass	Bradley et al. (2004)		
	Picloram + 2,4-D	0.30 + 1.12 kg ai/ha	(<i>Dactylis</i>)			

	Triclopyr + clopyralid	0.96 + 0.32 kg ai/ha	<i>glomerata</i> L.)	
	Triclopyr + clopyralid	1.26 + 0.42 kg ai/ha	and tall fescue (<i>Festuca</i> <i>arundinacea</i>)	
	2,4-D + triclopyr	2.20 + 1.12 kg ai/ha		
	Saflufenacil/dimethenamid-P + saflufenacil	735 + 25 g ai/ha	Corn (<i>Zea</i> <i>mays</i> L.) - PRE	Soltani et al. (2017)
	Saflufenacil/dimethenamid-P + dicamba/atrazine	735 + 1000 g ai/ha		
	Prosulfuron + dicamba	10 + 140 g ai/ha	Corn- POST	
Established	Glyphosate	2700 g ai/ha	Corn- PP	
	Glyphosate + imazethapyr	900 + 100 g ai/ha		
			Winter wheat (<i>Triticum</i> <i>aestivum</i> L.) - POST	Soltani et al. (2017)
	Prosulfuron + Bromoxynilb	10 + 140 g ai/ha		

	Glyphosate	1.68 kg ae/ha	-	Stachler & Kells
	Glyphosate + 2,4-D ester	1.68 + 0.56 kg ae/ha		(1997)
	2,4-D amine	1.1 kg ae/ha	-	Stachler et al.
	Metribuzin + Chlorimuron	297 + 28 g ai/ha	Soybean	
			(<i>Glycine max</i>	
			(L.) Merr)-	
	Linuron + Chlorimuron	563 + 31 g ai/ha	PRE	
			Soybean-	
Overwintered	Chlorimuron	12 g ai/ha	POST	Stachler & Kells
	MON 12000 + MON 13900 +	84 + 252 + 1,121 + 515 g		(1997)
	Pendimethalin + Paraquat	ai/ha	Corn- PRE	
	Atrazine	2,241 g ai/ha		
	CGA-152005	30 g ai/ha	Corn- POST	
	Flumetsulam + Clopyralid + 2,4-D	26 + 69 + 140 g ai/ha		

Abbreviation: ai-active ingredients; ae- acid equivalent; PP, PRE and POST denoted the preplant, preemergence and postemergence of targeted crops, respectively.

2.2.4 Conclusions and Recommendations

The main objective of this review is to understand the resilience of wild carrots to extreme climatic conditions and their implications on the cultivar purity of cultivated carrots through papers published in peer-reviewed journals or conference proceedings. Based on the findings, 64.71 % of the publications were published between 2013 and 2023, with studies focused primarily on countries in Europe (37.26 %) and North America (27.45 %). Country-wise analysis indicated that most of the studies were conducted in the United States (23.53 %) and the Netherlands (11.77 %). Furthermore, wild carrots have so far been reported in about 100 different countries worldwide. In the New Zealand context, invasion of wild carrot is comparatively higher in the North Island than in the South Island. Moreover, increased research efforts are needed to compare how wild and cultivated carrot pollen characteristics and behaviour respond to projected climate changes. This will provide insight into how pollen flow affects the future of commercial carrot seed production under climate change. The results of this study indicated that geographical regions have a significant influence on the phenology of wild carrots. As a result, it is essential to study the life history of wild carrots at the regional level, especially in New Zealand. Since wild carrots are becoming more adaptable to climate change, ongoing research will be helpful in developing sustainable weed management strategies and predicting potential geographical invasiveness. Furthermore, research findings on the level of outcrossing in carrots and their wild relatives, as well as the pollen movement associated with it, might be useful in developing strategies to reduce outcrossing-related issues. Even though the application of herbicides is one of the globally accepted strategies for controlling weed species, using herbicides to control the wild carrot population in or adjacent to the carrot seed-producing field is not possible yet. Thus, more research needs to be done to investigate if an herbicide regime can be used to eliminate a wild carrot

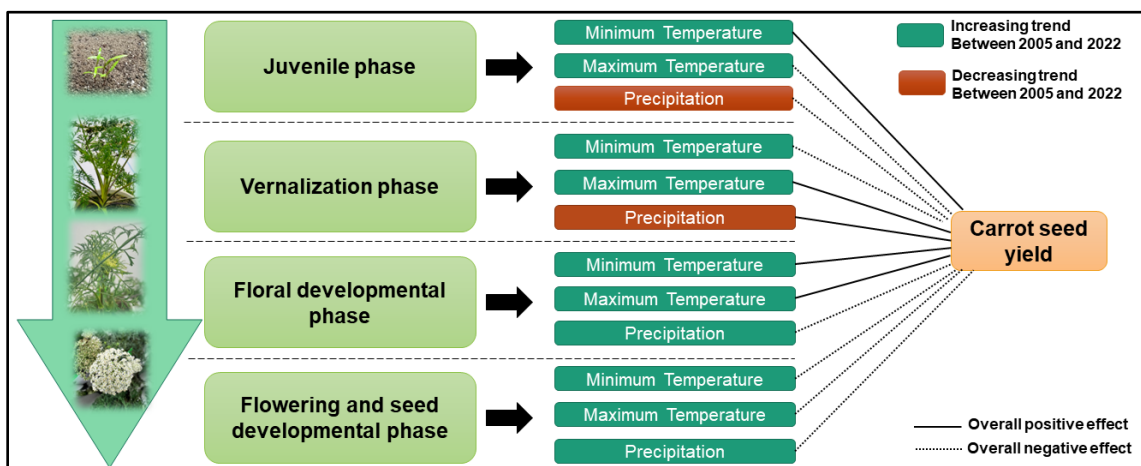
population from the carrot seed-producing fields. Furthermore, it is important to conduct field-related (quantitative) research to study how pollen-mediated gene flow from wild to cultivated carrots impacts the seed yield and quality of commercial carrot seeds. Based on this review, it is clear that wild carrots are mainly found in undisturbed land areas, which indicates that these weeds are mainly found in unpopulated regions. To encourage the involvement of the local community in the eradication process, it is imperative to create community awareness about invasive wild carrots. The findings of this systematic review help seed producers, policymakers, scientists, and farmers to evaluate the resilience of wild carrots to projected climate changes and to select appropriate weed management strategies to minimize the pollen flow from wild to cultivated carrots for the production of genetically pure commercial carrot seeds.

Chapter 3: Phenological phase affects carrot seed production sensitivity to climate change – A panel data analysis

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The literature review in Chapter 2 (2.1) revealed that the various phenological stages of carrot seed crops can be influenced by temperature and precipitation. However, there is a lack of research that demonstrates the impact of temperature and precipitation on various phenological stages of carrot seed crops in the context of seed production. Thus, the objective of chapter 3 is to determine the pattern of variations in the maximum and minimum temperatures as well as precipitation at various phenological stages of carrots. Furthermore, it aims to investigate the effect of climate change on New Zealand's carrot seed yield from 2005 to 2022.

Graphical abstract



Abstract

New Zealand is a major producer of carrot seeds globally. Carrots are an important nutritional crop for human consumption. Since the growth and development of carrot seed crops mainly depend on climatic factors, seed yield is extremely susceptible to climate change. This modelling study was undertaken using a panel data approach to determine the impact of the atmospheric conditions (proxied by maximum and minimum temperature) and precipitation during the critical growth stages for seed production in carrot, *viz.*, juvenile phase, vernalization phase, floral development phase, and flowering and seed development phase on carrot seed yield. The panel dataset was created using cross-sections from 28 locations within the Canterbury and Hawke's Bay regions of New Zealand that cultivate carrot seed crops and time series from 2005 to 2022. Pre-diagnostic tests were performed to test the model assumptions, and a fixed effect model was selected subsequently. There was significant ($p < 0.01$) variability in temperature and rainfall throughout different growing phases, except for precipitation at the vernalization phase. The highest rate of changes in maximum temperature, minimum temperature, and precipitation were recorded during the vernalization phase (+0.254 °C per year), floral development phase (+0.18 °C per year), and juvenile phase (-6.508 mm per year), respectively. Based on marginal effect analysis, the highest significant influence of minimum (187.724 kg/ha of seed yield decrease for each 1 °C increment) and maximum temperature (1 °C rise increases seed yield by 132.728 kg/ha), and precipitation (1 mm increment of rainfall decreases the seed yield by 1.745 kg/ha) on carrot seed yield were reported at vernalization, and flowering and seed development, respectively. The minimum and maximum temperatures have a higher marginal effect on carrot seed production. Analysis of the panel data demonstrates that the production of carrot seeds will be vulnerable to climatic change.

Keywords: Carrot seed crop, Marginal effect, New Zealand, Phenology, Regression, Seed yield

3.1 Introduction

Long-term variation in the behaviour of meteorological indices is known as climate change (Aliev et al., 2023; Jakob & Walland, 2016). The rising vulnerability of many nations to natural catastrophes due to climate change makes climate change a global issue (Boon Teck et al., 2021). Signals of ongoing climate change on a global scale are both understandable and unavoidable (Carroll & Aarrevaara, 2021; Chan et al., 2021). Changes in the pattern of atmospheric temperature and precipitation have been reported across the world (Guo et al., 2021; Todaro et al., 2022). Food security may also be adversely affected by climate change (Sinnarong et al., 2019). Agriculture depends on climatic conditions, particularly temperature and rainfall, hence, crop productivity is extremely sensitive to climate change (Zhang et al., 2022). Many researchers have modelled the impact of changing climatic factors on crop productivity, and have found that rising atmospheric temperatures and variations in precipitation affect both the quality and quantity of agricultural commodities (Abbas, 2022; Chaudhry & Sidhu, 2022; Warsame et al., 2021; Yerlikaya et al., 2020). A key requirement for food and nutritional security is the availability of high-quality seed in sufficient quantities when needed for crop production (Madin et al., 2022). Hence the impact of climate change on seed production also needs to be determined.

Geographical and soil conditions allow New Zealand to produce high-quality seeds for more than 50 different crops (Melhuish, 2008; Ministry of Foreign Affairs, 2017), including high-quality carrot seed, *Daucus carota* L. subsp. *sativus* to meet international demand (Aitken & Warrington, 2018; Broussard et al., 2017; J. Hampton et al., 2012; Selvakumar & Kalia, 2022). Around 50 % of the world's carrot seed is produced in New Zealand (Preece, 2023). Due to their biennial behaviour, carrots, a crop in the Apiaceae family, take about 13 months to complete the process of producing seeds (Junaid et al., 2023; Merfield et al., 2010). Carrot is grown in New Zealand

primarily in Canterbury but also in Hawke's Bay and is sown in New Zealand during summer for seed production. The cultivation season begins in February and finishes in March of the following year. Cool winter temperatures are an essential requirement to induce the flowering of carrots, which is easily achieved in New Zealand during June and July (Merfield et al., 2010). After the completion of the vernalization phase, the carrot starts to initiate floral development (Linke et al., 2019). In New Zealand, reproductive growth, including the development of floral organs and flowering, occurs generally between September to late February. Harvesting of carrot seeds is typically completed in March (Davidson et al., 2010; Howlett, 2012; Howlett & Gee, 2019). According to the variety, climate, management practices and geographical factors, the cropping calendar of carrot seed crops can marginally differ from region to region. Carrot, which is high in vitamin A, is regarded as an important vegetable for human consumption (Maurya et al., 2022). Due to its nutritive value and the increase in the global population, the consumption of carrots has climbed in recent years (Duran & Ipek, 2022). As a result, demand for carrots has increased around the world, creating a huge market for carrot growers and a consequent need for increased carrot seed supply (FAOSTAT, 2023; Galletti et al., 2020; Simon, 2019b).

Changes in temperature and precipitation can have an impact on each growing phase of a carrot seed crop (Broussard et al., 2017; Deleuran & Boelt, 2009). The influence of vernalization temperature on the rate of carrot flowering was demonstrated by Atherton et al. 1990, who noted that different temperatures during the vernalization period can significantly alter the success of flowering in carrot crops as shown in **Figure 2.4**. Likewise, Quagliotti (1967) and Hiller (1979) indicated the negative effect of temperature on floral stalk development of carrots. Furthermore, Broussard et al. (2017) and Chira et al. (2008) studied the behaviour of the carrot flower and floral parts in response to climate change and found a reduction in the performance of floral organs with

increasing temperature. In addition, Broussard et al. (2017) suggested components in carrot flowers that attract pollinators can be affected by higher temperatures, with a consequent effect on the foraging behaviour of pollinators. The impact of warm temperatures on the quality of carrot seeds was researched by Elballa & Cantliffe (1996), who found that the higher temperature during pollination, fertilization, and initial phases of seed development can significantly decrease the seed yield and seed quality of carrots. Germination and seedling growth of carrots can be inhibited by dry conditions caused by a lack of soil moisture and fewer extreme rainfall events (Andriamparany et al., 2020; Schmidhalter & Oertli, 1991). Soil moisture deficit is one of the important limiting factors in the production of quality taproots. A warmer, drier environment in carrot seed production areas will likely impact seed production (Jagosz et al., 2019; Lada et al., 2005; Léllis et al., 2017; Reid & Gillespie, 2017).

Consistent with an approximately linear trend during the 1970s, the world warmed by 0.25 °C from 2011 to 2021 (Robinson et al., 2021). New Zealand's average temperature has climbed by 1.13 ± 0.27 °C from 1909 to 2019. Furthermore, there has been an increase in the minimum and maximum temperatures during the winter compared with the past (Ministry for the Environment & Stats NZ, 2020). In New Zealand, the average atmospheric temperature is projected to increase by 0.8 °C in 2040, by 1.4 °C in 2090, and by 1.6 °C in 2110, compared to 1986-2005 under a mid-range estimation (Mullan et al., 2018). In regard to precipitation, the North Island of New Zealand is likely to receive less precipitation compared with the South Island (Climate Change Adaptation Technical Working Group, 2017). The southwestern and northeastern regions of the South Island are predicted to become wetter and drier, respectively (Caloiero, 2020; Macinnis-Ng et al., 2021). Furthermore, as a consequence, drought severity and flooding will be expected to intensify in New Zealand (Booth et al., 2020). These fluctuations in climatic variables could significantly affect

New Zealand's agriculture sector (Ausseil et al., 2021; Hopkins et al., 2015). Most extreme events expected to occur in New Zealand are related to changes in temperature and precipitation (Climate Change Adaptation Technical Working Group, 2017). Furthermore, most empirical papers estimating the empirical impacts of climate change on agricultural production employ measures of precipitation and temperature. The identification for the panel data approach comes from weather variation that is, in principle, random. Moreover, temperature and precipitation are potentially correlated and thus need to be included to avoid omitted variable bias (Dell et al., 2014). Consequently, this modelling study focussed on temperature and precipitation as variables.

Modelling approaches have been widely used as a tool to assess the impact of climate change on crop yield (Hasan & Kumar, 2021; Schmidt & Zinkernagel, 2017). These can be classified as process-based models and statistical models (Madhukar et al., 2021). Process-based models predict crop yield by simulating the physiological functions of a plant according to climatic factors, soil factors, management practices, and endogenous characteristics of plants (Chisanga et al., 2020; Crous-Duran et al., 2019; Stratonovitch et al., 2012). The inclusion of crop physiological mechanisms to determine the impact of weather on crop yield is an advantageous feature of process-based modelling. Though, utilizing process models for the predictions of an untested site (actual on-farm conditions) could cause unknown errors. This is due to using particular site-specific experimental data for the validation of the process-based models. Furthermore, factors such as the amount of fertilizer application, pest and disease incidences, and weed-control methods which are dependent on the behaviour of farmers cannot be accounted for in the process-based models (Roberts et al., 2017). The inaccessibility of reliable and complete historical data is also one of the constraints of using process-based modelling for climate change projections (Kephe et al., 2021). In contrast to the process-based model, the statistical model requires only historical

weather data and productivity data for particular crops for climate-crop modelling (Sinnarong et al., 2019). The statistical modelling approaches can be mainly classified as time series method, cross-section method and panel method (Lobell & Burke, 2010; Meerburg et al., 2009). The main strength of the panel data approach is the incorporation of time series dimension and cross-sectional dimension, which yields more precise model estimations than the other two methods ultimately (Hsiao, 2011). Furthermore, the panel data approach has the ability to control the unmeasured individual heterogeneity in the model. The presence of individual heterogeneity could bias the model parameters (Lockwood & McCaffrey, 2007).

Despite the production of carrot seeds in New Zealand being vital to the availability of high-quality carrot seeds when needed for the production of a carrot food crop, this is the first study conducted to analyse the effects of temperature and precipitation on carrot seed production using a panel data approach. There is a major research void in understanding how New Zealand's carrot seed yields will be impacted by climate change and how these can therefore be mitigated. The scientific aims of this panel data study are to identify the pattern of changes in maximum and minimum temperature, and precipitation at different phenological stages of carrots, and to determine the impact of climate change from 2005 to 2022 on carrot seed yield in New Zealand. Furthermore, the research hypothesizes that maximum and minimum temperature and precipitation are significantly affecting carrot seed yield during juvenile, vernalization, floral development, and flowering and seed development phases. This study provides baseline information to enable the development of mitigation strategies both in New Zealand and other carrot seed-producing areas of the world.

3.2 Material and methods

3.2.1 Study area and data acquisition

An unbalanced panel dataset was formed comprising 18 years from 2005 to 2022 and 28 regions (103 observations) of New Zealand. Regions from Canterbury (representing the South Island) and Hawke's Bay (representing the North Island) were included. The chosen regions represent an already well-established carrot-seed production region (Canterbury) and a developing carrot-seed production region (Hawke's Bay). To understand the effect of changes in temperature and precipitation during different phenological stages of carrots on seed yield, the study covered phenological stage-specific climatic variables. The juvenile phase, vernalization phase, floral development phase and flowering and seed development phase are also practically matched with autumn, winter, spring, and summer seasons, respectively. The region-wise monthly maximum temperature (T_{\max}), minimum temperature (T_{\min}) and precipitation were obtained from the national climate database, New Zealand (<https://cliflo.niwa.co.nz/>). To represent the climatic factors in the different phenological stages of carrots, the temperature and precipitation data were averaged and summed based on months relevant to each phenological stage. Similar studies by Liu et al. (2018) and Li et al. (2021) on changing climate and crop yields were used as a guide for the computation of these averages and summing over the phenological stages. Seed yield data from carrot seed-producing regions from 2005 to 2022 were obtained from South Pacific Seeds Ltd. South Pacific Seeds Ltd is one of the leading vegetable seed-producing companies in New Zealand. The precipitation, T_{\max} and T_{\min} were the explanatory variables, and the yield of carrot seeds was the response variable in the model. A description of the included explanatory variables in the panel data model is in **Table 3.1**.

Table 3.1 Description of considered variables in the panel model

	Phenological phase	Months	Variables considered	Notation
Vegetative growth	Juvenile • Vegetative growth	Feb- May	Minimum Temperature	JT_{\min}
			Maximum Temperature	JT_{\max}
			Precipitation	J_{pre}
	Vernalization • Transition from vegetative to reproductive phase	Jun- Aug	Minimum Temperature	VT_{\min}
			Maximum Temperature	VT_{\max}
			Precipitation	V_{pre}
Reproductive growth	Floral development • Induction of shoot meristem • Induction of flower meristem • Floral organ development	Sep-Dec	Minimum Temperature	FDT_{\min}
			Maximum Temperature	FDT_{\max}
			Precipitation	FD_{pre}
	Flowering and seed development • Pollination and fertilization • Seed formation and development • Seed harvesting	Jan-Mar (Following Year)	Minimum Temperature	FLT_{\min}
			Maximum Temperature	FLT_{\max}
			Precipitation	FL_{pre}
	Response variable		Carrot seed yield	Y

3.2.2 Model specification and estimation

According to previous studies (Busu, 2019; Pipitpukdee et al., 2020), this empirical study is suitable for regression modelling at the carrot-growing regional level to examine the relationship

between climatic variables and seed yield of carrots in New Zealand. We specify statistical yield as a function of climatic variables as shown in Equation 1:

$$\begin{aligned}
Y_{it} = & \beta_0 + \beta_1 JTmin_{it} + \beta_2 JTmin_{it}^2 + \beta_3 JTmax_{it} + \beta_4 JTmax_{it}^2 + \beta_5 Jpre_{it} + \beta_6 Jpre_{it}^2 + \\
& \beta_7 VTmin_{it} + \beta_8 VTmin_{it}^2 + \beta_9 VTmax_{it} + \beta_{10} VTmax_{it}^2 + \beta_{11} Vpre_{it} + \beta_{12} Vpre_{it}^2 + \\
& \beta_{13} FDTmin_{it} + \beta_{14} FDTmin_{it}^2 + \beta_{15} FDTmax_{it} + \beta_{16} FDTmax_{it}^2 + \beta_{17} FDpre_{it} + \\
& \beta_{18} FDpre_{it}^2 + \beta_{19} FLTmin_{it} + \beta_{20} FLTmin_{it}^2 + \beta_{21} FLTmax_{it} + \beta_{22} FLTmax_{it}^2 + \\
& \beta_{23} FLpre_{it} + \beta_{24} FLpre_{it}^2 + \alpha_i + \varepsilon_{it} \quad \rightarrow (1)
\end{aligned}$$

The i and t in Equation 1 denote region and time, respectively. The dependent variable Y_{it} is the carrot seed yield in the model, and the abbreviations of all the climatic explanatory variables used in the model are illustrated in **Table 3.1**. α_i represents the fixed effect summarizing time-invariant individual-specific heterogeneity, while ε_{it} indicates the error term. β_0 is the constant term, whereas β_1 to β_{24} denote the estimated coefficients for different independent variables. Previous literature stated that the effects of precipitation and temperature are mostly nonlinear (Konduri et al., 2020; Mishra et al., 2017). Therefore, the quadratic terms of T_{max} , T_{min} and precipitation were included in the statistical model along with the linear terms. Due to the presence of both linear and quadratic terms, a direct interpretation of single model coefficients may not be straightforward. Therefore, marginal coefficients of T_{max} , T_{min} and precipitation of different phenological phases were calculated at their mean values to determine the effect of climatic variables on carrot seed yield (Sharma et al., 2022).

3.2.3 Diagnostic tests

As a prerequisite to the panel data analysis, a set of diagnostic tests was conducted to confirm model assumptions. Non-stationary data (including a unit root) is unexpected and cannot be

predicted or modelled. The results acquired using non-stationary time series could be fictitious, implying a relationship between two variables where none exists (Sarker et al., 2014). Since the carrot seed panel dataset is made up of 18 years of observation, the time series data of each variable were checked to determine the presence of unit root (non-stationary) by performing Augmented Dickey-Fuller (ADF) test (Maddala & Wu, 1999), which is recommended to analyse unbalanced panel data set (Dimitrios et al., 2016).

Furthermore, the existence of heteroskedasticity may hinder the robustness of regression model results. Uniformity in the residual scattering across the regression line in a residual plot indicates homoscedasticity (Abbott & Gutgesell, 1994). The Breusch-Pagan test was performed to check for heteroscedasticity (Breusch & Pagan, 1979). The occurrence of strong correlations between independent variables makes it difficult to determine how each independent variable affects the dependent variable. Furthermore, panel data model estimation will be overfitted if the explanatory variables are correlated, which will lead to biased results. Therefore, a correlation matrix was used to study the relationship between the variables (Hysa et al., 2020; Jelonik et al., 2019). One of the assumptions of linear regression is the absence of autocorrelation, implying residuals are independent of one another. In the presence of positive autocorrelation, the actual standard error is underestimated by the estimated standard errors (Das, 2019). The Durbin-Watson test suggested by Bhargava et al. (1982) was performed to assess the presence of autocorrelation. The Hausman test (Hausman, 1978) was used to identify whether a fixed or random effect model is a probable fit for the panel data. The Hausman test determines if the estimators for fixed effects and random effects are significantly different, as well as the orthogonality between the random effects and the regressors (Hsiao, 2014). The collected data and estimated model were analysed with RStudio (version 2022.07.2 + 576).

3.3 Results and discussion

3.3.1 Descriptive statistics of variables

The summary statistics of variables included in the estimations are presented in **Table 3.2**. The average harvested carrot seed yield was recorded as 337.3 kg/ha. Due to the failure of the crop during some of the production seasons, the minimum yield was reported as zero. According to the historical climatic data, temperature and precipitation exhibited a significant variation across the different growth phases of carrot seed crops. The juvenile phase of the carrot begins from seed germination (Mandel & Brunet, 2019). Temperature above 30 °C reduced the germination of carrot seeds. Germination completely stopped in the temperature range from 40 °C to 45 °C (Corbineau et al., 1995; Pereira et al., 2007). In regards to physiological activities, Thiagarajan et al. (2007) found that the rate of net photosynthesis reduced by 23.7 % and transpiration increased by 118.9 % when increasing the temperature from 20 °C to 30 °C. The findings confirmed that the temperature ranges from 8.15 °C to 19.30 °C during the juvenile phase have a beneficial influence on seed germination and physiological activities in New Zealand's carrot-growing regions. Also, Wurr et al. (1998) observed that the fresh weight of carrot roots increased along with temperature increment up to 15.5 °C, before declining at a higher temperature. The findings of this study showed that the mean temperature during the juvenile phase is 13.73 °C ($[JT_{\min} + JT_{\max}]/2$), which is several degrees lower than 15.5 °C and favourable for the growth of the roots. Additionally, dry conditions due to a lack of soil moisture and fewer intense rainfall events can impact carrot germination, seedling growth, photosynthesis, and transpiration processes (Andriamparany et al., 2020; Schmidhalter & Oertli, 1991; Thiagarajan et al., 2008). Comparatively, the second-highest amount of precipitation was seen during the plant's juvenile stage, confirming that carrots need to

have access to soil moisture during their early growth phases (Dellow et al., 2016; Jagosz et al., 2019).

New Zealand mostly uses biennial cultivars to produce carrot seed. The optimum requirement of cold temperature for successful vernalization is 5 °C for 11 to 12 weeks (Linke et al., 2019). This requirement is important for the induction of floral formation via the incremental increase in gibberellic acid within the plant (Nieuwhof, 1984; Ou et al., 2017). The findings (**Table 3.2**) showed that vernalization occurred from June to August (Southern Hemisphere's winter months), coinciding with a mean temperature of about 7 °C ($[\text{VT}_{\min} + \text{VT}_{\max}]/2$); this temperature is beneficial for the successful vernalization and, consequently, flower development (Atherton et al., 1990). Carrot flower development begins with the formation of a floral stalk (bolting), followed by the production of involucre bracts and umbel primordia (Hiller & Kelly, 2019; Linke et al., 2019). Quagliotti (1967) observed a significant decrease in flower stalk development when increasing the temperature from 14 °C to 26 °C. Elballa and Cantliffe (1996) noted that the increasing temperature from 17/12 to 33/28 °C reduced the total number of umbels per plant by 44 %. However, according to the historical temperature data, 12.91 °C ($[\text{FDT}_{\min} + \text{FDT}_{\max}]/2$), the temperature that prevailed during the time of carrot flower development is suitable for the floral stalk development and umbel formation.

The carrot pollination process has also been affected by environmental impacts (Gaffney et al., 2018; Howlett, 2012). Previous studies showed that the warmer temperature (30 °C) reduced the receptive period of stigma, which can negatively affect the fertilization process (Chira et al., 2008). Furthermore, Broussard et al. (2017) suggested that increasing temperatures may have an impact on carrot flower attributes that attract pollinators, including nectar concentration and volatile emission. Pollinators' subsequent foraging behaviour may be impacted as a result of this. Elballa

& Cantliffe (1996), also reported that exposing carrot seed crops at anthesis or before seed development to a warm temperature (33/28 °C) could adversely affect the seed yield and seed quality of carrots. Whereas the seeds produced at 20/15 °C exhibited comparatively higher progeny vigour and germination than seeds formed and developed at 33/28 °C. However, the minimum (10.87 °C) and maximum (22.37 °C) temperature that existed during the flowering and seed development phase, is appropriate for the pollination, fertilization, and production of high-quality carrot seeds. Moreover, this phase overlaps with the warmest and driest season in New Zealand. Comparatively less precipitation, 163.50 mm (see **Table 3.2**), at the time of the flowering and seed development phase compared with the other phases, will minimize fungal and bacterial infections during the flowering and seed development (Deleuran & Boelt, 2009).

3.3.2 Pre-estimation diagnostic tests

A correlation matrix of the variables used in the panel model is shown in **Figure 3.1**. Hysa et al. (2020) claimed that the initial indication of significant multicollinearity is the presence of a very high correlation between the variables, which is typically considered to be 0.85-0.90 or greater. The results of the estimated correlation (**Figure 3.1**) revealed that there was no problematic correlation between the variables. **Table 3.3** shows the results of the Augmented Dickey-Fuller (ADF) unit root test. According to the estimated test statistics, climate and carrot seed yield variables reveal similar results with and without a time trend. Furthermore, this implies that, for all variables in the table, the null hypothesis of unit roots (i.e., non-stationary) is rejected at the 5 % level of significance. The conclusion is that all the variables are stationary, and that differencing is redundant. As shown in **Table 3.4**, the panel model had a p -value of 0.7735 for the Breusch–Pagan–Godfrey test, which was not statistically significant ($p > 0.01$) and revealed that the null hypothesis of homoscedasticity can be accepted. Furthermore, the result of the Durbin-Watson test

(2.4) proved the lack of serial correlation in the model (**Table 3.4**). This conclusion was made by incorporating the suggestion of Field (2009), who stated that values of the Durbin-Watson test statistic from 1 to 3 are relatively normal. Based on the Hausman test results (**Table 3.4**), the fixed effect model was selected for the model estimation by rejecting the null hypothesis (H_0 : random effects model is suitable, H_a : random effects model is not suitable) at 1 % significance level (Hausman, 1978).

Table 3.2 Descriptive statistics on yields and climate variables (2005 - 2022)

Variables	Unit	Mean	Std.Dev	Maximum	Minimum
JT _{min}	°C	8.15	1.28	11.73	4.45
JT _{max}	°C	19.30	1.49	22.78	16.38
J _{pre}	mm	236.90	90.33	518.90	78.20
VT _{min}	°C	2.21	1.26	4.73	-1.23
VT _{max}	°C	12.23	1.58	15.70	8.37
V _{pre}	mm	190.50	77.70	421.90	47.50
FDT _{min}	°C	7.38	1.21	10.48	3.530
FDT _{max}	°C	18.44	1.34	21.55	16.23
FD _{pre}	mm	240.60	88.13	512.90	77.20
FLT _{min}	°C	10.87	1.44	15.90	7.67
FLT _{max}	°C	22.37	1.55	25.73	19.50
FL _{pre}	mm	163.50	76.80	453.00	40.20
Y	kg/ha	337.30	260.58	1080.80	0.00

Note: Std.Dev- Standard deviation

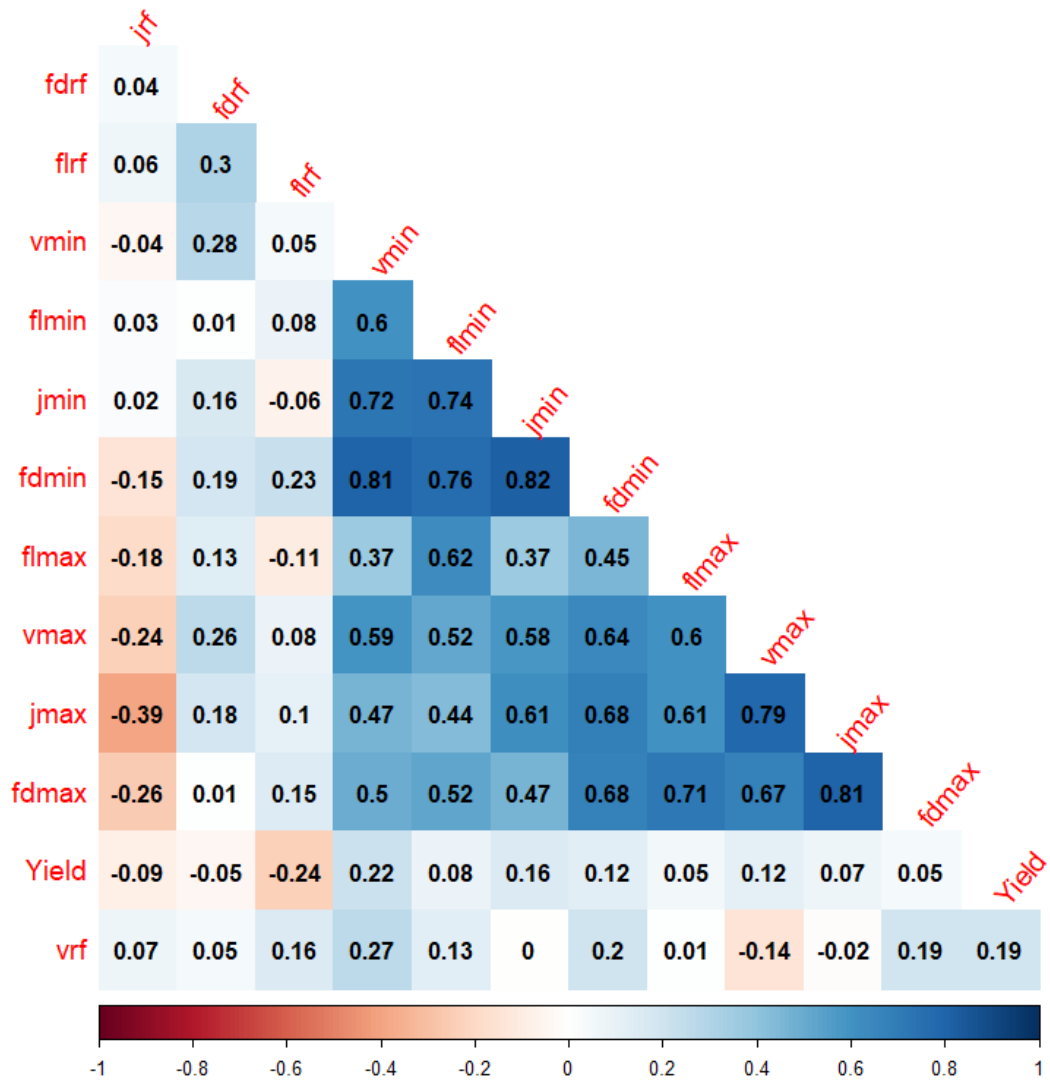


Figure 3.1 Pearson correlation matrix of variables

Table 3.3 Results of unit root test

Augmented Dickey-Fuller Test				
Variables	With trend		Without trend	
	Test statistics	<i>p</i> -value	Test statistics	<i>p</i> -value
JT _{max}	-3.590	0.000	-0.450	0.000
JT _{min}	-4.117	0.000	-0.523	0.009
J _{pre}	-5.291	0.000	-1.181	0.000
VT _{max}	-2.805	0.000	-0.632	0.001
VT _{min}	-3.480	0.000	-1.568	0.005
V _{pre}	-6.457	0.000	-1.181	0.000
FDT _{max}	-3.965	0.000	-0.361	0.000
FDT _{min}	-4.466	0.000	-0.691	0.016
FD _{pre}	-4.583	0.000	-1.013	0.000
FLT _{max}	-3.485	0.000	-0.234	0.000
FLT _{min}	-4.489	0.000	-0.447	0.025
FL _{pre}	-7.899	0.000	-1.543	0.000

Table 3.4 Results of model specification tests

Specification tests	Value
<i>Heteroscedasticity tests</i>	
Breusch–Pagan–Godfrey test	18.589
(<i>p-value</i>)	0.7735
<i>Serial correlation test</i>	
<i>Durbin–Watson test statistic</i>	2.4
(<i>p-value</i>)	0.9907
<i>Hausman test (Fixed effect vs Random effect)</i>	
Chi-square value	49.459***
(<i>p-value</i>)	<0.001

Note *** Specifies that the significance at 1 %; Breusch–Pagan–Godfrey test indicates the *F*-statistic

3.3.3 Observed climate trends across carrot seed crop-growing regions in New Zealand

The observed climatic trends are shown in **Figure 3.2**. Throughout the carrot seed crop growing season (CSGS), the T_{\max} and T_{\min} showed a similar increasing trend. This is further validating the warming trends already reported for New Zealand (Ministry for the Environment & Stats NZ, 2020). By the middle of the 21st century, the New Zealand region's mean air temperature is predicted to have increased by +1.0 °C compared with 1995-2014, and by 2100, it is predicted to have increased by +1.6 °C under Shared Socioeconomic Pathways (SSPs) 2- 4.5. In the middle and at the end of the century, the expected increases in mean air temperature for SSP5-8.5 are +1.3 °C and +3.1 °C in comparison with 1995-2014, respectively (Bodeker et al., 2022). Furthermore,

precipitation has exhibited an increasing pattern during the reproductive stages (floral development, and flowering and seed development phases) and a decreasing trend during vegetative ones (juvenile and vernalization phases) over the past 18 years in New Zealand. These findings were further supported by Ministry for the Environment (2018), which stated that projected changes in precipitation exhibit a clear seasonality and regional variability in New Zealand. Furthermore, all climatic variable trends were found to be significant ($p < 0.01$), except for precipitation ($p=0.3914$) during the vernalization phase in CSGS.

Table 3.5 indicates the annual rate of change in climatic variables. The values of maximum and minimum temperature, and rainfall varied throughout the juvenile phase of the CSGS by $0.2\text{ }^{\circ}\text{C}$ (T_{\max}), $0.134\text{ }^{\circ}\text{C}$ (T_{\min}), and -6.508 mm , while during vernalization, they changed by $0.254\text{ }^{\circ}\text{C}$, $0.168\text{ }^{\circ}\text{C}$, and -1.105 mm . Moreover, the rate of changes in T_{\max} ($0.147\text{ }^{\circ}\text{C}$), T_{\min} ($0.180\text{ }^{\circ}\text{C}$) and precipitation (5.041 mm) at the floral development stage increased significantly ($p < 0.01$) over time. During the flowering and seed development phases, the rate of changes in maximum and minimum temperatures and precipitation were respectively $0.159\text{ }^{\circ}\text{C}$, $0.165\text{ }^{\circ}\text{C}$ and 3.508 mm , from 2005 to 2022. In accordance with Ministry for the Environment (2018), the study area is on the east of both islands, which includes Hawke's Bay and Canterbury, where conditions are likely to be wetter (increasing trend) during the summer (flowering and seed development phase) and drier (decreasing trend) during winter (vernalization phase). The phenological phases of vernalization, floral development, and juvenile, accordingly, were associated with the largest rates of changes in T_{\max} , T_{\min} , and precipitation.

Commonly, it is believed that the temperature and precipitation changes have a significant influence on seed germination (Corbineau et al., 1995; Pereira et al., 2007), seedling establishment (Ibrahim et al., 2006), vernalization (Atherton et al., 1990), taproot development (Gomes et al.,

2020; Zeipiņa et al., 2014), photosynthesis (Thiagarajan et al., 2012), floral development (Samuolienė et al., 2008), pollination (Broussard et al., 2017) and seed formation (Gray et al., 1988; Hooda et al., 2013) in carrots. Furthermore, the activities of pollinators also have been altered by these climatic factors (Howlett, 2012). Based on these long-term trends in weather variables, T_{\max} , T_{\min} and precipitations can influence carrot seed production during the growing season in New Zealand by altering the physiological and flowering processes. To mitigate changes in weather variables, multiple responses will be essential including the development and introduction of new varieties through plant breeding strategies, geographic shifts and adapting climate-smart agronomic practices (Franke et al., 2022; Vandamme et al., 2022; Xiong et al., 2022).

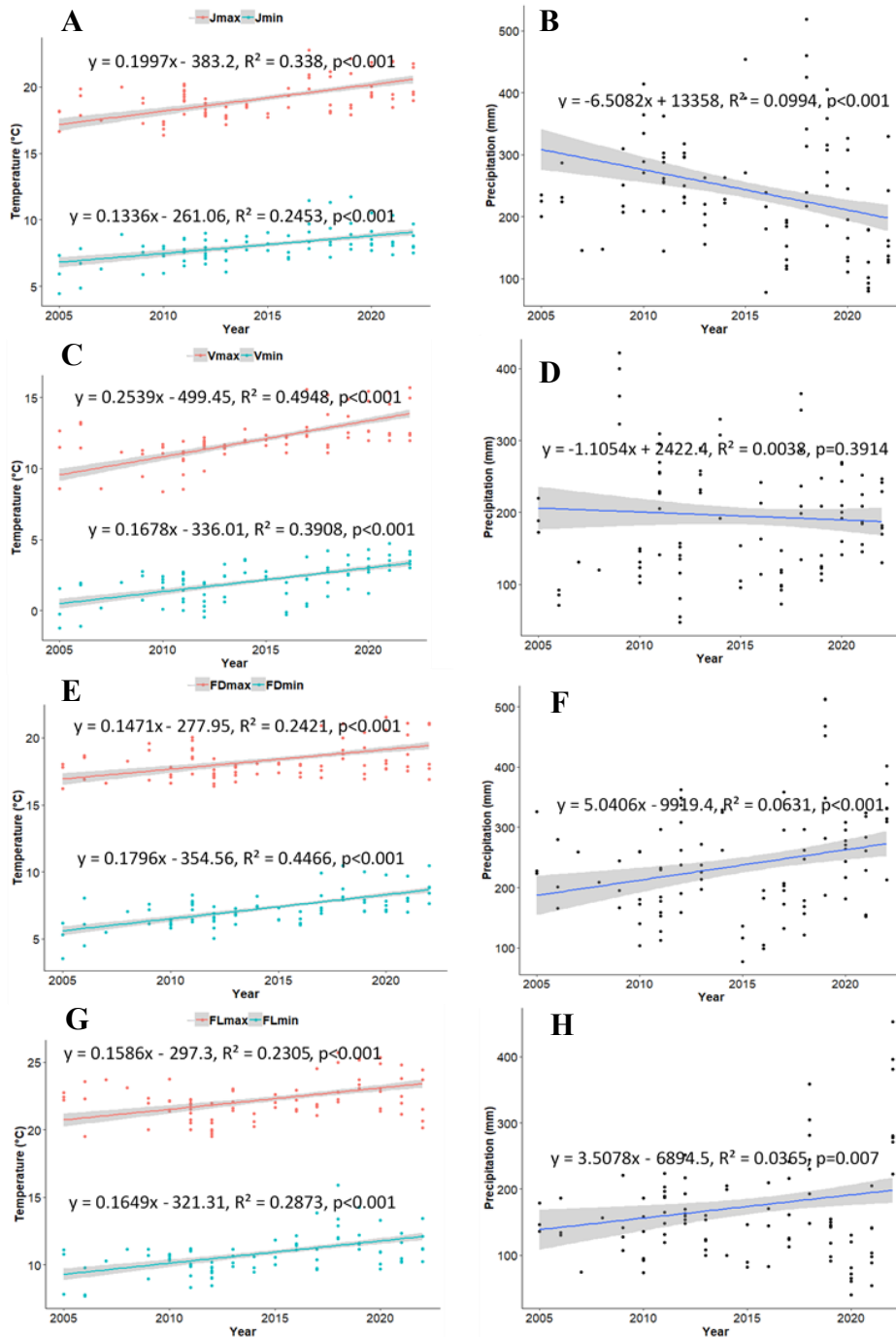


Figure 3.2 Temperature and precipitation during the different phenological phases. (A) and (B)- juvenile phase (Feb to May); (C) and (D)- vernalizing phase (Jun to Aug); (E) and (F)- floral development phase (Sep to Dec); (G) and (H)- flowering and seed development

Table 3.5 The annual rate of change occurred in temperature and precipitation from 2005 to 2022 during the carrot seed crop growing season in New Zealand

Climatic Variable	Rate of change in climatic variables per year (2005-2022)
Juvenile phase	
T _{max} (°C)	0.200 ^{***}
T _{min} (°C)	0.134 ^{***}
Precipitation (mm)	-6.508 ^{***}
Vernalizing phase	
T _{max} (°C)	0.254 ^{***}
T _{min} (°C)	0.168 ^{***}
Precipitation (mm)	-1.105
Floral development phase	
T _{max} (°C)	0.147 ^{***}
T _{min} (°C)	0.180 ^{***}
Precipitation (mm)	5.041 ^{***}
Flowering and seed development phase	
T _{max} (°C)	0.159 ^{***}
T _{min} (°C)	0.165 ^{***}
Precipitation (mm)	3.508 ^{***}

*Note: *** 0.01 level of statistical significance*

3.3.4 Effect of changes in temperature and precipitation on carrot seed yield

The estimates of the influence of seasonal temperature and precipitation on carrot seed yield by using the fixed effect model are presented in **Table 3.6**.

In general, the juvenile phase of carrots includes seed germination and vegetative growth along with leaf and taproot development (Geoffriau & Simon, 2020). During the juvenile phase of carrot seed crops, the regression coefficient of JT_{\min} was shown to be negative and significant. Whereas the quadratic term of JT_{\min} exhibited a significant positive trend. Moreover, the study results illustrated that the JT_{\max} had a beneficial effect on carrot seed yield, while the effect of JT_{\max}^2 was found to be negative and significant on the seed production of carrots. These findings indicated that the trend of maximum and minimum temperature is nonlinear during the juvenile stage of carrot seed crops, which agrees with a recent similar maize and cotton study (Sharma et al., 2022). The higher temperature can interrupt the metabolic and enzymatic activities held during germination (Dias et al., 2015; Nascimento et al., 2008). Moreover, the reduced germination due to the increase in temperature stress during the germination period may result in heterogeneous growth in plants along with substandard emergence, which could cause variation in the maturity of the seed crops. Carrot is an indeterminate crop and therefore flowers continuously. A narrow flowering time is crucial for high yields of seeds with the same maturity. Ultimately, the quality of the seed harvested will be reduced by uneven production in the field due to uneven maturity (Nascimento et al., 2008; Tetteh et al., 2018). Moreover, Hussain et al. (2008) noted that a temperature increase beyond 20 °C can result in a decline in plant vegetative matter during the juvenile phase, which has a significant impact on the production of carrot seeds. Likewise, increasing temperature beyond 25 °C has a commensurate increase in the rate of respiration with resultant poor root yield (Rubatzky et al., 1999). Reduced root size (yield) typically results in less

food storage, which will potentially impact seed development and seed production (Ilyas et al., 2013). The negative (J_{pre}) and positive (J_{pre}^2) signs of the precipitation coefficients have shown that rainfall during the juvenile phase of carrot seed crop has a significant ($p < 0.01$) U-shaped relationship with carrot seed yield, that is, as rainfall increases, carrot seed yield decreases, but only up to a certain point after which it starts increasing. This may be due to the varying degrees of sensitivity of different sub-phases (germination, seedling establishment, and root development) of the juvenile stage to precipitation. Deficits in soil moisture can reduce the germination of seeds and seedling emergence by altering the imbibition rate, delaying the mobilization of food reserves and metabolic activities in the germinating seed, and inhibiting plumule and radicle elongation. Consequently, delayed germination and seedling growth could result in poor root growth (Lada et al., 2004) and, in turn, reduced seed production. For uniform seedling emergence, it is beneficial for the optimum precipitation to coincide with the radicle initiation and seed germination times (Finch-Savage & Phelps, 1993). On the other hand, excessive rainfall or flooding can lower the amount of oxygen that is available in the soil profile, which causes stress for seed germination and seedling emergence (Zhou et al., 2020). Previous studies have shown that when the drought has prevailed for 10 days, the carrot seedlings reach their permanent wilting stage. Furthermore, 7 days of drought reduced the soil moisture by 43 %, which decreased the xylem pressure potential by 67 % approximately (Rajasekaran & Blake, 2002). These effects, individually or combined, are likely to lower the yield of carrot seeds.

Climatic factors play a key role in the transition from the vegetative stage to the reproductive stage via vernalization by initiating various changes to the morphological and physiological processes in carrots (Alessandro et al., 2013; Liu et al., 2020; Siswadi et al., 2021). The results (see **Table 3.6**) illustrated that the VT_{max} and VT_{max}^2 are not significant ($p > 0.1$). While only the VT_{min}^2 had

a significant ($p < 0.01$) and negative influence on the carrot seed yield. This finding is in accordance with the results of Atherton et al. (1990), who reported that increments of temperature from $-1\text{ }^{\circ}\text{C}$ to $5\text{ }^{\circ}\text{C}$ increased flowering of carrots, while a significant decline was observed when increasing the temperature from $7\text{ }^{\circ}\text{C}$ to $16\text{ }^{\circ}\text{C}$. In New Zealand, vernalization of carrots occurs from June to August, the three coldest months (Abraham et al., 2022; Pole, 2003). This is one of the key reasons for the non-significance of vernalization temperature (VT_{max} and VT_{min}) on carrot seed yield. The overall 18-year averaged VT_{max} , $12.23\text{ }^{\circ}\text{C}$ and VT_{min} , $2.21\text{ }^{\circ}\text{C}$ (see **Table 3.1**) fall under the values of $14.6\text{ }^{\circ}\text{C}$ and $6.6\text{ }^{\circ}\text{C}$, which are considered as the ceiling values for maximum and optimum temperature, for the vernalization of carrot (Weikai & Hunt, 1999). The impact of precipitation during the vernalizing phase has been found to be beneficial ($p < 0.05$), whereas the quadratic term is negative and not significant ($p > 0.1$). This suggests that the result is linear. However, any damage caused due to the excess precipitation at the time of vernalization is minimal to carrot seed yield because the plant is still in the vegetative phase. A similar effect on the linear and squared term of rainfall was reported for the productivity of pigeon peas in India (Mishra et al., 2017) and Aus-type rice in Bangladesh (Sarker et al., 2014). Reid & Gillespie (2017) observed that increasing soil water deficit reduced storage root fresh yield of carrot cv Chantenay Red Core by $(0.30 \pm 0.025)\text{ t ha}^{-1}\text{ mm}^{-1}$ in New Zealand. Root size is an influencing factor on carrot seed yield (Ilyas et al., 2013). Similarly, previous studies showed that the soil moisture level below -60 cbar significantly reduces root yield. This reduction could be due to the dysfunction of physiological activities under water stress conditions (Lada & Stiles, 2014). These findings indicated that the soil moisture deficit, even during vernalization can alter the size of the taproot, which ultimately affects the carrot seed yield (Kumar et al., 2017).

There was no significant ($p > 0.1$) relationship between carrot seed yield, and maximum temperature (except FLT_{\min} and FLT_{\min}^2) and precipitation during floral development and flowering and seed development (both in linear and quadratic terms) (see **Table 3.6**). This could be due to the presence of optimum maximum temperature and precipitation during floral development, pollinator activities, fertilization, and seed development throughout the reproductive phase from 2005 to 2022. However, this situation could change due to predicted future climate change. Whereas FLT_{\min} and FLT_{\min}^2 variables have exhibited a significantly positive and negative effect on carrot seed yield, respectively (see **Table 3.6**). Increasing temperature is detrimental to carrot seed production due to its adverse effect on the pollination process, altering the growth, development and performance of plant reproductive parts, flower reward production and foraging activities of pollinators (Descamps et al., 2018; Ramírez & Kallarackal, 2018; Thakur et al., 2010). Most early studies revealed that increments of temperature from 20/10 °C to 30/20 °C significantly reduced the average weight of a single seed. Although the weight of the embryo and endosperm has not been affected, the pericarp weight decreased with increasing temperature (Gray et al., 1988), again reducing yield. In New Zealand, Broussard et al. (2017) studied the effect of increasing temperature on hybrid carrot seed production and discovered that increasing temperature reduced the volatile production and increased the concentration of nectar sugar, which may minimize the attractiveness of insect pollinators.

Table 3.6 Panel regression results for carrot seed yield response

Variables	Regression Coefficient	Standard error	t-value	p-value
JT _{max}	1403.100*	801.74	1.750	0.086
JT _{max} ²	-39.634*	21.31	-1.860	0.069
JT _{min}	-1362.600***	401.58	-3.393	0.001
JT _{min} ²	84.507***	24.50	3.449	0.001
J _{pre}	-4.801***	1.67	-2.876	0.006
J _{pre} ²	0.008***	0.00	2.683	0.010
VT _{max}	-188.420	595.09	-0.317	0.753
VT _{max} ²	13.133	25.49	0.515	0.609
VT _{min}	168.990	153.38	1.102	0.276
VT _{min} ²	-80.892***	29.40	-2.752	0.008
V _{pre}	4.117**	2.04	2.019	0.049
V _{pre} ²	-0.007	0.00	-1.596	0.117
FDT _{max}	-134.060	1029.00	-0.130	0.897
FDT _{max} ²	4.492	27.87	0.161	0.873
FDT _{min}	441.980	406.84	1.086	0.282
FDT _{min} ²	-17.687	27.64	-0.640	0.525
FD _{pre}	1.278	1.40	0.915	0.364
FD _{pre} ²	-0.003	0.00	-1.248	0.218
FLT _{max}	181.010	889.48	0.204	0.840
FLT _{max} ²	-4.258	20.36	-0.209	0.835
FLT _{min}	567.630*	321.34	1.766	0.083
FLT _{min} ²	-29.448**	14.55	-2.023	0.048
FL _{pre}	-2.711	1.66	-1.638	0.108
FL _{pre} ²	0.003	0.00	0.817	0.418

Note: *, ** and *** specify that the significant at the 10 %, 5 % and 1 %, respectively

3.3.5 Marginal effects

The average marginal effects of a 1°C rise in temperature and of a 1 mm increase in rainfall (BIRTHAL et al., 2014) on carrot seed yield are shown in **Table 3.7**.

The average marginal effect of JT_{max} was shown to be negative and significant ($p < 0.1$) during the CSGS, indicating a 126.76 kg/ha decrease in carrot seed yield for every 1°C increase in its value. As suggested by Hussain et al. (2008), carrot is highly sensitive to temperature rise during photosynthesis, and root and plant partitioning, which can negatively affect seed production. The average marginal effect of JT_{min} had no significant ($p > 0.1$) effect on the seed yield of carrots. This shows that the minimum temperature at the juvenile stage of the CSGS is generally favourable for the growth and development of carrots and their seed production. Moreover, it was determined that the MCR of J_{pre} was unfavourable ($p < 0.05$), resulting in a reduction of 1.038 kg/ha in carrot seed production for every increase in rainfall of 1 mm. A 1°C rise in VT_{min} significantly dropped the carrot seed yield by 187.724 kg/ha. In contrast, VT_{max} positively and significantly influenced the seed yield by increasing it by 132.728 kg/ha for each 1°C increment. Similarly, carrot seed yield benefitted significantly from the rise in V_{pre} , where an increase in 1 mm rainfall has boosted the seed yield by 1.327 kg/ha. Carrot seed crop shows a statistically significant increase in seed yield during the floral development phase when increasing the minimum temperature (FDT_{min}), i.e., 180.832 kg/ha increase in seed yield with a 1 °C increase in FDT_{min} . Hiller & Kelly (1979) noted that an increase in post-vernalization (6 weeks) temperature to 27/32 °C affected floral stalk elongation in carrots, though the floral differentiation has not been affected adversely. Similar observations were reported by Elballa & Cantliffe (1996), who found an increase in day/night temperature from 17/12 °C to 33/28 °C decreased flower stalk height and number of umbels per plant from 73 cm to 55 cm and 50 to 28, respectively. However, over the past 18 years of CSGS,

the minimum and maximum temperatures during floral development ranged from 3.53 °C to 10.48 °C and 16.23 °C to 21.55 °C, respectively (see **Table 3.2**), which are far below the ceiling limit for the destruction of flower organs. This could be one of the reasons for the positive relationship between FDT_{min} and carrot seed yield. The average marginal effect of FDT_{max} and FD_{pre} are statistically not significant for carrot seed yield. The marginal effects of FLT_{max} and FLT_{min} have been found to be positive, though non-significant ($p > 0.1$). With a decrease of 1.745 kg/ha for every 1 mm, FL_{pre} has had a negative and significant ($p < 0.01$) impact on carrot seed production. This result agrees with Lawson & Rands (2019), who show that changes in rainfall pattern cause nectar dilution, pollen degradation and affects pollinator activities.

The marginal effects analysis indicated that precipitation has a significantly (except for FD_{pre}) lower marginal effect than minimum and maximum temperature. A similar trend was observed by Mishra et al. (2017) on pigeon peas and by Sharma et al. (2022) on cotton and soybean. The highest unfavourable effect from precipitation has been reported at the flowering and seed development phase, while only the vernalization phase is favoured by the precipitation compared with other phases.

Table 3.7 Marginal effects of climatic variables on carrot seed yields

Variables	Marginal coefficient of regression	Standard error	z- value	p-value
JT _{min}	14.820	82.608	0.179	0.858
JT _{max}	-126.760*	72.779	-1.742	0.082
J _{pre}	-1.038**	0.521	-1.991	0.046
VT _{max}	132.728*	77.970	1.702	0.089
VT _{min}	-187.724**	81.041	-2.316	0.021
V _{pre}	1.327**	0.553	2.399	0.016
FDT _{max}	31.629	68.799	0.460	0.646
FDT _{min}	180.832*	97.791	1.849	0.064
FD _{pre}	-0.119	0.550	-0.215	0.829
FLT _{max}	-9.575	61.717	-0.155	0.877
FLT _{min}	-72.640	58.749	-1.236	0.216
FL _{pre}	-1.745***	0.663	-2.630	0.009

Note: *, ** and *** specify that the significant at the 10 %, 5 % and 1 %, respectively

3.4 Conclusion

The main objective of this study was to evaluate the effects of changes in minimum temperature, maximum temperature, and precipitation on the seed yield of carrots using an unbalanced panel data model. Based on the results of diagnostic tests, a fixed effect model was utilized to estimate the impacts. The use of fixed effect model is appropriate because it accounts for all time-invariant omitted variables in the model. Historical climatic data highlighted the increasing trends in the rate of changes in minimum and maximum temperature in the eastern region of both the North and South Islands of New Zealand, where carrots are grown for seed production, throughout the season. The rate of changes in precipitation was negative during the vegetative (February to August) and positive during the reproductive (September to March) stages of carrot seed growth. These patterns

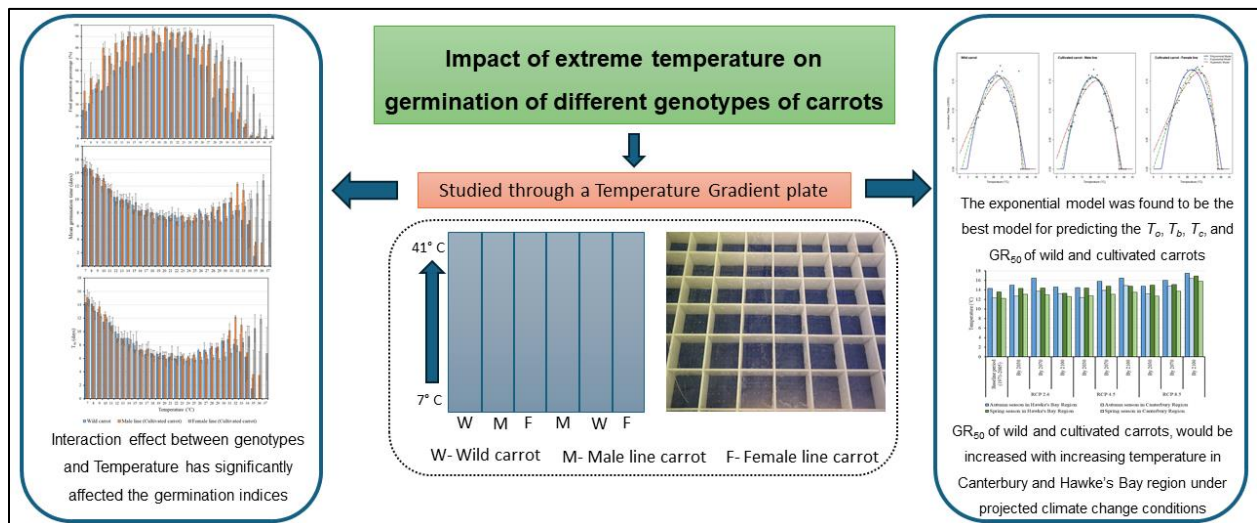
have value for the prediction and mitigation of future extreme climatic effects on carrot seed production. Consistent with the existing results, increasing rainfall was found to be unfavourable to the seed yield throughout the phenological stages except during vernalization. On the other hand, the rising pattern of maximum temperature during the juvenile phase, and flowering and seed development exhibited a negative effect on carrot seed yield. A 1 °C rise in maximum temperature at vernalization and floral development is estimated to be beneficial. Meanwhile, the increment of minimum temperature over juvenile and floral development has an advantageous effect on seed yield. In contrast, a 1 °C rise in minimum temperature at vernalization, and flowering and seed development was found to be detrimental to seed production. These results lead to the conclusion that the degree to which temperature and rainfall affect carrot seed yield depends on the different phenological stages and on whether they are minima or maxima. Meanwhile, marginal effects of maximum and minimum temperatures are having a higher impact on carrot seed yield. Furthermore, it is clear that the growth and development, and physiological activities beginning from seed germination to harvest influence carrot seed yield. These suggest the importance of formulating and adapting phenological stage-specific climate change strategies to cope with future climate change. This work further offers data for important policy choices, such as the development of climate-resilient carrot seed crops via biotechnological techniques, identifying possible carrot seed production sites, and adaptation of precision agriculture practices in response to climate change.

Chapter 4: Modelling germination response of wild and commercial carrot (Apiaceae) seeds to temperature from the perspective of climate change

This chapter is currently under review in the *Horticulture, Environment, and Biotechnology*

The literature review in chapter 2 and the findings of chapter 3 revealed that temperature is one of the most significant factors that can affect the germination of both cultivated carrots and wild carrots. Consequently, reduced germination capacity caused by elevated temperature stress during the germination phase may lead to heterogeneous growth in cultivated carrots. Furthermore, wild carrots can exhibit extensive variation in germination due to their wide adaptability. However, research is lacking on the relationship between the germination patterns of different *Daucus carota* subspecies and the temperature gradient. Therefore, the objective of chapter 4 is to model the relationship between the germination of cultivated carrots, including male and female lines, and wild carrots across a temperature gradient.

Graphical abstract



Abstract

Globally, climate change poses a serious threat to the seed germination of wild and cultivated carrots, as increasing atmospheric temperatures can affect the optimal conditions required for germination. Successful germination is crucial since it results in the development of healthy plants capable of producing flowers and seeds subsequently. However, there are still limited studies on how the range of temperature gradient impacts the germination of male and female lines of cultivated carrots and wild carrots, which compete with male lines of cultivated carrots in terms of pollen flow in hybrid carrot seed production. Therefore, a germination assay was conducted to model the relationship between the germination of carrot male line and female line, and wild carrots across a range of constant temperature by using a temperature gradient plate. This study was laid out in a strip plot design with four replications with each replicate consisting of 25 seeds. The results show that the temperature, genotype, and their interactions had a significant effect ($P < 0.05$) on germination percentage, mean germination time, and time to reach 50 % germination. The highest germination occurred at 20 °C for cultivated carrots, with 98 % for male and 97 % for female lines, and at 21 °C for wild carrots (87 %). Based on higher R^2 , and lower $RMSE$, and AIC , the exponential model was selected to determine the cardinal temperatures for the seed germination of wild and cultivated carrots (including male and female lines). The values of base, optimum, and ceiling temperatures of wild, and cultivated carrots ranged from -0.22 to 2.98 °C, 22.11 to 25.55 °C, and 37.88 to 38.64 °C, respectively. Based on climate change projections, the germination rate ($GR_{50} = 1/\text{time required for 50 \% of the total seeds to germinate}$) of wild and cultivated carrots is likely to increase with rising temperatures in Canterbury and Hawke's Bay regions. By 2100, under the RCP 8.5 scenario, increasing temperature are predicted to accelerate the seed germination by increasing GR_{50} , as temperatures fall inside the suboptimal temperature range. In Canterbury

region, the highest variations in GR₅₀ for male and female lines of cultivated carrots and wild carrots, including winter and summer annual, are predicted as 25.67 %, 26.88 %, 26.37 %, and 23.83 %, respectively. In conclusion, carrot seed industries must cope with increasing temperatures, as climate change accelerates germination rates of wild and cultivated carrots.

Keywords: *Daucus carota*; Germination indices; Hybrid carrot; Logistic function; Regression; Temperature gradient plate

4.1 Introduction

Daucus carota is an important species in the family Apiaceae with over 60 intraspecific taxa, consisting of both cultivated (*Daucus carota* L. subsp. *sativus*) and wild carrot (*Daucus carota* subsp. *carota*) (Spooner, 2019). Cultivated carrots are one of the top 10 vegetables as the source of dietary vitamin A, which is essential for eyesight, pre-and postnatal development, immune functions, and healthy skin (Hufnagl & Jensen-Jarolim, 2019; Kokande et al., 2024; Simon, 2019a). In contrast, wild carrots are considered an invasive weed globally, compromising the genetic purity of commercial carrots through undesirable pollen flow (Godwin et al., 2024b). Furthermore, wild relatives of carrots consist of greater genetic diversity, allowing them to survive in a variety of adverse abiotic challenges, such as heat, drought, and salinity conditions (Mezghani et al., 2024). Therefore, it is important to conduct comprehensive comparisons between wild and cultivated carrots of their growth performance during various phenological stages, such as seed germination, vegetative growth, floral development and flowering, and seed production. This comparison will deliver significant insights into their respective resilience to climate change, helping to recognize which varieties or subspecies are better equipped to withstand abiotic stresses.

Seed germination is an important stage in the life cycle of carrots, and extremely sensitive to climate change, with temperature playing a critical role (Bolton et al., 2019; Mahmood-ur-Rehman et al., 2024). The optimal germination temperatures range between 20 °C and 30 °C (Dias et al., 2015; Nascimento et al., 2008). At this optimal range, temperature facilitates the seed germination via enabling faster enzymatic activities and metabolic pathways. At optimal temperatures (20–30 °C), enzymatic activities, such as those of proteases and amylases, are maximized, leading to efficient mobilization of stored carbohydrates and proteins, which support seed germination and seedling development (Dias et al., 2015; Nascimento et al., 2008). Conversely, the germination capacity of carrot seeds is reduced at temperatures above 30 °C, whilst germination can be completely inhibited at temperatures between 40 °C and 45 °C, emphasizing the importance of temperature regulation for effective seed germination (Corbineau et al., 1995; Pereira et al., 2007). Due to climate change, global mean temperature has already risen by 1.1 °C. Under the business-as-usual scenario (RCP 8.5), global surface temperature increases may cross 1.5 °C by 2040 and reach as high as 3.5 °C by 2100 (Pathak, 2022). This could have a significant impact on the seed germination rate and percentage of carrot species (Godwin et al., 2023). Thus, understanding the impact of temperature extremes on the germination of carrot seeds, including male and female lines (generally used in hybrid carrot seed production as paternal and maternal lines, respectively), is an important aspect of the development of adaptation strategies to climate change. Moreover, studying the germination patterns of wild carrots in comparison to cultivated carrots is essential for the development of efficient weed management strategies under extreme climatic conditions (Bolton et al., 2019). These objectives can be investigated through studying the germination patterns of wild and cultivated carrots across a continuous temperature gradient under controlled laboratory conditions using a temperature gradient plate (TGP).

Temperature gradient plates (generally known as thermogradient plates or thermal gradient plates) have been used to investigate the pattern of seed germination across an extensive range of temperatures since the 1950s (Collette et al., 2022). Conducting the same experiment with germination incubators would require a series of incubators, emphasizing the importance of utilizing TGP over incubators. Using numerous incubators requires significant financial and space resources, particularly for studies involving a range of temperatures in seed germination (Welbaum et al., 2016). Usually, a TGP is made using a flat aluminium plate that has heating elements at one edge and a cooling component at the other end (Newbery et al., 2020). The working area of TGP is essentially divided into 196 miniature incubators with distinct temperature regimes by a detachable Perspex matrix placed on top of the aluminium plate (Stevens et al., 2014). Accordingly, the Perspex matrix divides the temperature gradient generally from 5 to 50 °C, which is favourable for climate-based research. Furthermore, this range of temperature facilitates making more precise estimates of climate change impacts on seed germination compared with using separate germinators (Cochrane, 2016).

Based on previous literature, it is clear that the TGP is one of the effective research tools for studying the relationship between germination responses of plant species and climate change. For example, a study by Filipe et al. (2023) demonstrated that a TGP can effectively estimate the impact of global warming on the germination response of two different Mediterranean-type climate forest species (*Eucalyptus marginata* and *Corymbia calophylla*). They found *Eucalyptus marginata* is more vulnerable to global warming than *Corymbia calophylla*. Similarly, Collette et al. (2022) modelled the germination patterns of three different tree species, *Callitris baileyi*, *Wollemia nobilis*, and *Alectryon subdentatus* by using the TGP and they revealed the sensitivity of *C. baileyi* and *A. subdentatus* to seasonal temperature variations. Moreover, Cochrane (2019,

2020) has used the TGP to study the impact of projected climate change on the germination responses of endemic native plant species in Australia, potentially facilitating the formulation of management measures to conserve these species. These studies collectively demonstrate the significance and applicability of using TGPs in seed research in the context of climate change. Simultaneously, precise estimation of the impact of temperature variabilities on seed germination patterns is made possible by the incorporation of thermal time modelling approaches into TGP studies (Alvarado & Bradford, 2002; Dahal et al., 1990; Zhang et al., 2013).

Generally, thermal time (TT) models (known as threshold models) are used to interpret seed germination in the context of cardinal temperatures, including ceiling (T_c), base (T_b), and optimal (T_o) temperatures (Amin et al., 2023; Batlla & Bencech-Arnold, 2015). Furthermore, Onofri et al. (2018) stated that TT models are primarily formulated based on the assumption that the germination does not take place below the T_b or above T_c . Whereas, the GR_{50} ($GR_{50} = 1/\text{time}$ required for 50 % of the total seeds to germinate) reaches its peak at the optimum temperature (T_o) (Correa et al., 2021). Identifying the thermal thresholds (T_b , T_c , and T_o) is becoming more prevalent for predicting the survival of plant species in regards to climate change, which emphasise the significance of using TT models (Duarte et al., 2018; Huang et al., 2016; Liu et al., 2020). Incorporation of time-to-event models in seed germination studies, which includes the TT modelling, is comparatively more advantageous than conventional linear/nonlinear regression modelling since the time-to-event methods are typically effective in handling statistical peculiarities inherited in germination assays (Onofri et al., 2018, 2022).

Previous studies about seed germination of carrots, including wild and cultivated carrots, have not often modelled the response of germination with a wide range of temperature gradients by using a TGP. However, incorporating TT modelling with germination responses of wild and cultivated

carrots is crucial for understanding their resilience to extreme temperatures more precisely. Even though hybrid carrot seed production in New Zealand is important to the global seed market, no study, to the author's knowledge, has been conducted to analyse the impact of temperature on seed germination of carrot genotypes, including wild and cultivated carrots, found in New Zealand, using the TT modelling approach with a TGP. There is a significant research gap in determining how seed germination of wild and cultivated carrots found in New Zealand will be affected by climate change and how these can impact survival and distribution. This research on the seed germination of wild and cultivated carrots in New Zealand can provide valuable insights applicable to production environments in the Northern Hemisphere, as similar climatic changes may affect germination, survival, and distribution patterns of wild and cultivated carrots globally. The primary objectives of this germination study were to quantify the seed germination of wild and cultivated carrots found in New Zealand, to validate the effectiveness of different threshold models, including exponential, polynomial, and hyperbolic models, to estimate the temperature thresholds, and to relate it with projected climate change. The findings from this research provide the baseline insights into how extreme temperature (temperatures outside the optimal range of 20 - 30 °C) may affect the seed germination of wild and cultivated carrots, offering useful information for researchers, industries and stakeholders to develop climate-resilient commercial carrot varieties, formulate weed management strategies to control wild carrots and make timely decisions for enhancement of carrot seed production.

4.2 Material and methods

4.2.1 Seed material

This study focused on two subspecies, including cultivated carrots (*Daucus carota* L. subsp. *sativus*) and wild carrots (*Daucus carota* subsp. *carota*) of the family Apiaceae. The seed material comprising No. 27 CMS female line and the No. 27 pollinator male line of carrots was obtained from South Pacific Seeds (NZ) Ltd, a hybrid vegetable seed company in New Zealand. On the other hand, seeds of wild carrots were collected from Dairy Farm One, located at Massey University in Palmerston North, New Zealand (40°22'31.0"S 175°36'21.3"E) in May 2022. Prior to the experiment, these seeds were stored at 5 °C for a year. The initial germination percentage of all the genotypes was examined to identify any dormancy of the seed. The result of the preliminary germination test is shown in **Table 4.1**. Along with the preliminary germination tests, a cut test was performed to check the viability of the seeds, and the results indicated that most of the seeds were viable. Due to the presence of seed dormancy, 0.2 % KNO₃ solution was used to moisten the seed germination blotters instead of water at the beginning of the experiment (ISTA, 2023). The primary objective of this study was to compare the cardinal temperature requirements for germination in wild and cultivated carrots and to predict their responses under future climate change. To achieve this, seed dormancy was broken to minimize this as a confounding effect and confirm that observed differences in germination were attributed to sensitivity of temperature rather than dormancy behaviour.

Table 4.1 Initial and post-KNO₃ application germination percentage of wild and cultivated carrots at 20 °C

Genotype	Initial Germination percentage	Germination percentage after KNO₃ treatment
Wild carrot	44.00 %	80 %
Female line (CMS type)	81.13 %	92 %
Male line (OP type)	74.92%	90.4 %

4.2.2 Seed germination testing

Germination experiments were conducted in the Seed Laboratory, School of Agriculture and Environment, Massey University, Palmerston North, New Zealand from May 2023 to August 2023. A Temperature Gradient Plate (TPG, Model GRD1, Grant Instruments, Cambridge, UK) was used to model the germination behaviour of different carrot genotypes, including male and female lines of cultivated carrots and wild carrots, across a range of temperatures. The TGP method is used to evaluate a larger spectrum of responses to future temperature scenarios and detect thresholds more precisely than step-wise temperatures given by incubators. Furthermore, TGPs provide a stable and consistent temperature gradient, reducing the variability that might occur with separate incubators. The TPG was set to run a one-way gradient, using a temperature range of 7 °C to 41 °C. Based on previous literature, the temperature range and one-way gradient were selected for this study (Bolton et al., 2019; Nascimento et al., 2012; Pereira et al., 2007). Due to the lack of space on the TGP, only 2 replicates could be studied per run. Therefore, the trial was repeated 2 times to obtain data from all 4 replicates (McGill et al., 2000).

The surface of the TGP was sterilized by using 70 % ethanol. Multilayers of Kimpack[®] papers were soaked in distilled water and placed on the plate surface (McGill et al., 2000). The paper's edges were tucked into troughs on the plate's four sides. Subsequently, germination blotters were soaked in 0.2 % KNO₃ solution and placed on top of white blotters. A 14 x 14 Perspex grid, with 51.4 x 51.4 mm cells was placed onto the seed blotters. The temperature on the plate was allowed to stabilize and thermostats were used to confirm the temperature range had stabilized and whether the set temperatures had been reached. The TGP was placed in the laboratory where the seeds were exposed to natural daylight. Blotters were regularly replenished by spraying a small amount of water as needed throughout the experiment.

4.2.3 Data collection and calculation of germination indices

Germinated seeds were scored daily for the radicle emergence over a 21-day period. Upon each counting, the germinated seeds were removed to facilitate observation and to avoid recounting (Sousaraei et al., 2022). A seed was scored as germinated when the radicle has emerged and has a length of more than 1 mm (Bolton et al., 2019). The main reason for selecting radicle emergence over normal seedling development is that seedling development might be affected by severe temperature conditions. Furthermore, seedling growth might vary significantly due to post-germination conditions (such as moisture availability and energy reserves), making it less reliable for determining the direct impact of temperature on germination.

The scored data were used to calculate the following germination indices,

1. Final germination percentage (FGP) was calculated by using **Eq 1**.

$$FGP (\%) = \frac{n}{N} \times 100 \rightarrow \mathbf{Eq\ 1}$$

Where n = Number of germinated seeds, and N = Total number of tested seeds

2. Mean germination time (MGT) was calculated according to Cochran et al. (2014) by using

Eq 2.

$$MGT = \frac{\sum(n_i \times d_i)}{N} \rightarrow \text{Eq 2}$$

Where n_i = number of germinated seeds in each scoring interval, d_i = number of days from sowing to the end of particular interval, and N = total number of germinated seeds.

Following dormancy breaking with KNO_3 , germination percentage increased across all seed lots; hence, the number of germinated seeds was used as the denominator (N) to calculate MGT (Cochran, 2019).

3. Time to reach 50 % germination (t_{50}) was calculated according to Coolbear et al. (1984) by using **Eq 3.**

$$t_{50} = T_i + \frac{(\frac{N+1}{2} - N_i)(T_j - T_i)}{N_j - N_i} \rightarrow \text{Eq 3}$$

Where, N = total number of germinated seeds, N_i and N_j are the total number of germinated seeds in adjacent counts at time T_i and T_j accordingly, when $N_i < \frac{N+1}{2} < N_j$

4. Median germination rate (GR_{50}) was calculated according to Masin et al. (2017) by using **Eq 4.**

$$GR_{50} = \frac{1}{t_{50}} \rightarrow \text{Eq 4}$$

4.2.4 Experimental design

The TGP experiment was executed in a strip-plot design with two factors, including temperature and genotype. In this strip-plot design (**Figure 4.1**), the TGP area is divided into long strips based on temperature gradient, with each strip planted with different genotypes (Salinas Ruíz et al., 2024)

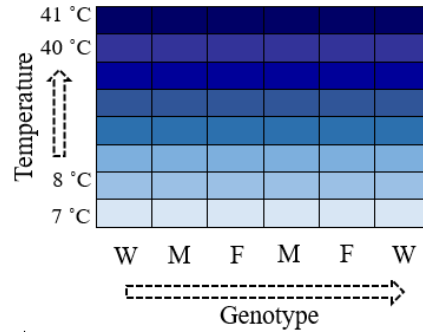


Figure 4.1 Arrangement the strip-plot design with two factors (temperature, and genotypes); W- Wild carrot, M- male line (cultivated carrot), and F- female line

4.2.5 Estimation of cardinal temperatures

As shown in **Table 4.2**, the polynomial, exponential, and hyperbolic models were used to determine the cardinal temperatures for the germination of wild and cultivated carrots, including male and female lines.

Table 4.2 Polynomial, exponential, and hyperbolic models were fitted to the germination rate of wild and cultivated carrots vs temperature

Model	Formula	Reference
Polynomial	$GR = \frac{\max[T, T_b] - T_b}{\theta_T} \left[1 - \frac{\min[T, T_c] - T_b}{T_c - T_b} \right]$	Mesgaran et al. (2017)
Exponential	$GR = \frac{\max[T, T_b] - T_b}{\theta_T} \left[\frac{1 - \exp[k(\min[T, T_c] - T_c)]}{1 - \exp[k(T_b - T_c)]} \right]$	Masin et al. (2017)

Hyperbolic	$GR = \frac{\max[T, T_b] - T_b}{\theta_T} \left[1 - \frac{q \frac{\min[T, T_c] - T_b}{T_c - T_b}}{1 + (q - 1) \frac{T - T_b}{T_c - T_b}} \right]$	Kropff & van Laar, (1993)
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Note: GR, germination rate; T , temperature; T_b , base temperature; T_c , ceiling temperature, θ_T , thermal time; k , switch-off parameter; q , coefficient

4.2.6 Thermal time

$$\theta_T = (T - T_b)t \quad T_b < T < T_o$$

T_b = base temperature, T_o = optimum temperature T = Temperature, and t = time taken for the germination of 50 % of seeds, θ_T = thermal time (°C.days)

4.2.7 Future climate projections

The projected seasonal (autumn, and spring) climatic data of temperature were extracted from the “Our Future Climate New Zealand” (OFCNZ) web tool for each year from 1971 to 2100 (NIWA, 2023). Climate data for Christchurch (to represent the Canterbury region) and Napier (to represent the Hawke's Bay region) were retrieved to accurately reflect the study area. The key reason for choosing Christchurch and Napier as representative locations, instead of specific carrot seed growing regions such as Ashburton, was the availability of data from OFCNZ. The projected climatic data were obtained for the HADGEM2–ES General Circulation Model (GCM). The incorporation of HADGEM2–ES as the GCM to this study was encouraged by previous works in New Zealand and Australia (Atalah et al., 2022; Ivković et al., 2016; Santillán et al., 2019). Projected climatic outcomes for three different representative concentration pathways (RCPs), consisting of a mitigation pathway (RCP 2.6), a stabilization pathway (RCP 4.5), and a continual increase pathway (RCP 8.5), were obtained from HADGEM2-ES in order to account for potential fluctuations in temperatures due to future CO₂ concentration (IPCC, 2013; Neverman et al., 2023).

Climate change models typically use atmospheric temperature due to its widespread availability and strong correlation with upper soil layer temperatures where germination occurs (Fernández-Pascual et al., 2015). Furthermore, there are currently no climate change projections available for soil temperature in New Zealand.

4.2.8 Statistical analysis

Initially, collected data were subjected to analysis of variance (ANOVA) for the strip-plot design to find out the interaction effect of temperature and genotypes on different germination indices. Consequently, mean separation was conducted using the least significant difference (LSD) test at a 5 % significance level ($p < 0.05$). R package ‘germinationmetrics’ was used to compute the germination indices. Polynomial, exponential, and hyperbolic models were fitted to the observed data by using the R package ‘drcSeedGerm’ (Onofri et al., 2018). Coefficient of determination (R^2), root mean square error ($RMSE$), and Akaike information criterion (AIC) were used to compare the fitted models with observed data. All the statistical analysis was conducted by using Rstudio (version 2022.07.2 + 576).

4.3 Results and discussion

4.3.1 Impact of temperature on germination of wild and cultivated carrots

The two-way ANOVA indicated (**Table 4.3**) that temperature (T), genotype (G), and their interactions ($G \times T$) had a significant effect ($P < 0.05$) on final germination percentage (FGP), mean germination time (MGT), and time to reach 50 % germination (T_{50}). The results of the LSD test for the FGP, MGT, and T_{50} are shown in **Figure 4.2**.

Table 4.3 Analysis of variance of the effects of temperature on different genotypes of carrots

Source of variation	df	Mean square		
		FGP	MGT	T ₅₀
Replicate	3	723.5 ^{ns}	51.43 ^{ns}	51.60 ^{ns}
Genotype (G)	2	13879.7 ^{**}	27.06 ^{**}	24.42 ^{**}
Temperature (T)	30	13552.5 ^{**}	154.56 ^{**}	147.85 ^{**}
G × T	57	336.2 ^{**}	11.24 ^{**}	11.27 ^{**}

Note: df, Degrees of freedom; FGP, Final germination percentage; MGT, mean germination time; T₅₀, time to reach 50 % germination. ^{ns}, ^{*}, and ^{**} are non-significant, and significant at 0.05, and 0.01 probability levels, respectively.

4.3.1.1 Effect of temperatures on seed germination capacity

Seed germination percentage is an important index in germination studies investigating different temperatures and genotypes as it delivers significant insights into seed viability and seedling emergence under different environmental conditions (Sousaraei et al., 2021). **Figure 4.2A** demonstrates the variation of germination percentages from wild and cultivated carrots across a temperature gradient from 7 °C to 37 °C. The germination percentages of wild and cultivated carrots increased as the temperature increased to the optimal one at which the highest germination percentage was reported and then declined as the temperature rose further. A similar finding was reported by Motsa et al. (2015) on different species of African leafy vegetables and by Fakhfakh et al. (2024) on annual grass *Stipa capensis*. Generally, enzymatic activities increase with temperature until it reaches the optimum temperature, accelerating the biochemical process required for seed germination. Conversely, when temperatures climb above the optimum range,

enzyme activities may become extremely high or enzymes may denature, resulting in a decline in germination percentage (Xue et al., 2021). In addition, extreme temperatures can accelerate abscisic acid (ABA) production and suppress the synthesis of gibberellic acid (GA), causing cellular and embryo death (Sharma et al., 2022; Toh et al., 2008). Furthermore, heat stress leads to increased production of reactive oxygen species (ROS), and in response, carrots activate antioxidant enzymes such as catalase (CAT), peroxidase (POD), and superoxide dismutase (SOD) to mitigate oxidative damage and maintain cellular function. Excessive production of ROS can cause oxidative damage to DNA, proteins, and lipids, leading to degradation of membranes, and cellular dysfunction. As a result, level of antioxidant enzymes can be decreased in carrots germinated under heat stress conditions (Mahmood-ur-Rehman et al., 2024). The highest germination percentage was observed at temperatures of 20 °C for cultivated carrots, including male (98 %) and female (97 %) lines, and 21 °C for wild carrots (87 %). However, there were no significant ($p > 0.05$) differences among these treatment combinations. In similar studies, 85 % of 'Brasília' carrot seeds germinated at 20 °C (Pereira et al., 2008), whereas Nascimento et al. (2012) reported that seed germination of 29 commercial cultivars was above 80 % at 25 °C. Moreover, more than 80 % of seed germination occurred in male lines between 12 °C and 27 °C, and in female lines between 13 °C and 27 °C. In comparison, wild carrots had > 80 % germination within a narrower temperature range between 19 °C and 23 °C (except at 20 °C). On the other hand, seed germination was entirely suppressed at temperatures above 35 °C for wild carrots, 36 °C for the male line, and 37 °C for the female line (**Figure 4.2A**), which emphasises the importance of optimal temperature in the germination process of carrot seed. These findings are consistent with the finding of Corbineau et al. (1994), who noted that the carrots can be germinated in a wide range of temperatures from 5 °C to 35 °C. However, cold temperatures 5 °C - 10 °C and temperatures

above 30 °C can reduce the germination of carrots (Corbineau et al., 1995). Furthermore, it was observed that the germination percentage of wild carrots was lower than the cultivated lines across the entire temperature gradient (**Figure 4.2A**). The lower germination percentage of wild relatives compared to cultivated types can be due to the domestication of cultivated carrots to germinate more uniformly, presence of dormancy in seeds of wild relatives, and environmental adaptations (Sedláková et al., 2021). Even though this study (Chapter 4) used only one seed lot per genotype, similar results have been observed in broader experiments; for instance Bolton et al. (2019) noted that the wild carrots have shown significantly lower germination than the cultivated carrots at 25 °C (by 2 %) and 35 °C (by 20 %) across 60 wild and 200 cultivated accessions from different regions of the world. These findings suggest that the ability of carrot seeds to germinate at different temperatures is at least partially dependent on the genotype (Nascimento et al., 2008). In the same context, Sharma et al. (2022) found differences in the genetic potential of different wheat genotypes to survive under temperature fluctuations.

4.3.1.2 Effect of temperatures on speed and time of seed germination

Mean germination time (MGT) is one of the key metrics in seed trials since it represents the mean time required for the germination of seeds (Ullah et al., 2022). The effects of temperature on MGT and T_{50} of wild and cultivated carrots are shown in **Figure 4.2B** and **Figure 4.2C**, respectively. The lowest MGT (rapid germination) was observed at temperatures of 25 °C for wild carrots (6.8 days), 22 °C for male lines (6.7 days), and 23 °C for female lines (6.6 days) within the temperature range of 7 °C - 31 °C. Meanwhile, the lowest T_{50} was recorded at temperatures of 24 °C for wild carrots (5.7 days), 22 °C for male lines (5.9 days), and 29 °C for female lines (5.7 days). The key reason for the significant variation in temperature to reach the lowest T_{50} between the male and female cultivated carrot lines in particular is likely due to genetic differences among the genotypes.

Furthermore, the MGT and T_{50} of wild and cultivated carrots declined as the temperature rose to the optimal after which speed of germination decreased further (**Figure 4.2B** and **Figure 4.2C**). This might be due to the rapid mobilization of seed reserves along with increasing temperature (Sharma et al., 2022). These findings are consistent with observations made by Parvez (2022), who reported that the temperature increment from 15 °C to 23 °C (in the below optimal range) reduced the MGT of carrot seeds from 3.4 days to 3.0 days. Similarly, Suzuki et al. (1993) stated that the temperature increment from 7 °C to 25 °C reduced the MGT from 13.0 days to 2.9 days for the ‘Shinkuroda Gosun’ carrot variety and 15.6 days to 3.7 days for the ‘Early Chantenay’ carrot variety. In the context of MGT, the female lines (6.6 days) germinated more rapidly than the wild (6.8 days) and male lines (6.7 days) of carrots within the temperature range of 20 °C - 25 °C (**Figure 4.2B**). There was a decline in MGT and T_{50} at temperatures over 35 °C in wild carrots (**Figure 4.2A**). This might be due to the extreme temperatures that can accelerate the germination initially, stress the seeds, and lower the overall germination percentage. In this context, any confounding bias caused by genotype-specific dormancy was minimized by improving germination percentages across all three genotypes following KNO_3 treatment. These findings have similarities with Marques et al. (2014), who observed a significant fluctuation in the MGT of *Racinaea aerisicola* seeds as the temperature increased from 15 °C to 35 °C.

In the New Zealand context, identifying the relationship between temperature and carrot seed germination is important for finding the optimal period of seed sowing in New Zealand, where climatic conditions vary widely between the regions. Carrot is cultivated mainly for its taproot as a vegetable, as well as for seed production when planted as a seed crop (Loarca et al., 2024). Hence, the timing of seed sowing for carrots differs depending on whether they are cultivated for taproot production or seed production. This study mainly aimed at seed production, which is why

it included male and female lines of cultivated carrots and wild carrots. In New Zealand, carrot seed production is largely carried out in the Canterbury and Hawke's Bay regions, where the carrot seed is typically sown in February (Bhatia, 2023; Godwin et al., 2023). Over the last decade, the average atmospheric temperature of February has been approximately 17.36 °C in Canterbury (based on Christchurch Aero Club meteorological data) and 19.65 °C in Hawke's Bay region (based on Hastings Aws meteorological data) (<https://cliflo.niwa.co.nz>). Furthermore, from 1991 to 2020, the average soil temperature during February was approximately 17.1 °C in Christchurch (representing the Canterbury region) and 20.1 °C in Napier (representing the Hawke's Bay region) (NIWA, 2023). The findings from this study confirmed that the current sowing time (February) is beneficial for the seed germination of male and female lines of cultivated carrots in carrot seed-producing regions in New Zealand. Furthermore, infestation of wild carrots is abundant in the Canterbury and Hawke's Bay regions of New Zealand (Bhatia, 2023). Unlike cultivated carrots, wild carrots can establish themselves as a winter annual or summer annual due to their wide life history strategies in New Zealand (**See Chapter 6**). Consequently, seed germination of winter annuals and summer annuals occurs in the autumn and spring seasons, respectively (Mandel & Brunet, 2019). According to the temperature data from the past 10 years, the average autumn temperature in Canterbury is around 12.42 °C and spring temperature is approximately 11.75 °C. On the other hand, Hawke's Bay experienced an average autumn temperature of around 14.92 °C and spring temperature is approximately 14.22 °C (<https://cliflo.niwa.co.nz>). Based on these findings, it is evident that the wild carrot can reach seed germination between 46 % - 64 % at current temperatures during the autumn and spring seasons (~11 °C - ~15 °C) in Canterbury and Hawke's Bay regions. Thermal time models can be used to investigate how projected temperature rise in carrot seed producing regions can affect the seed germination of cultivated and wild carrots.

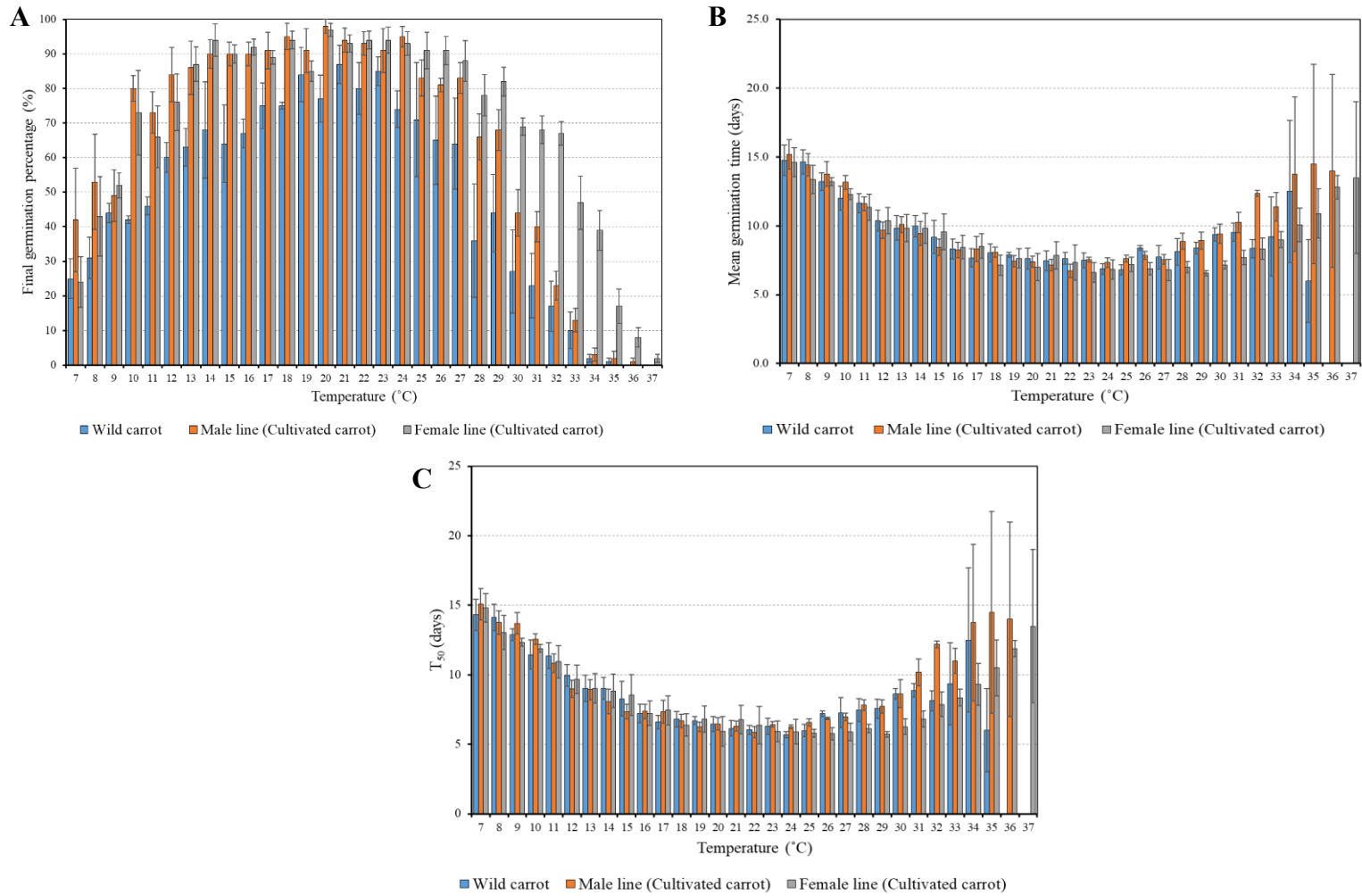


Figure 4.2 Interaction effect of genotype and temperature on FGP (A), MGT (B), and T_{50} (C). Vertical bars represent standard error value

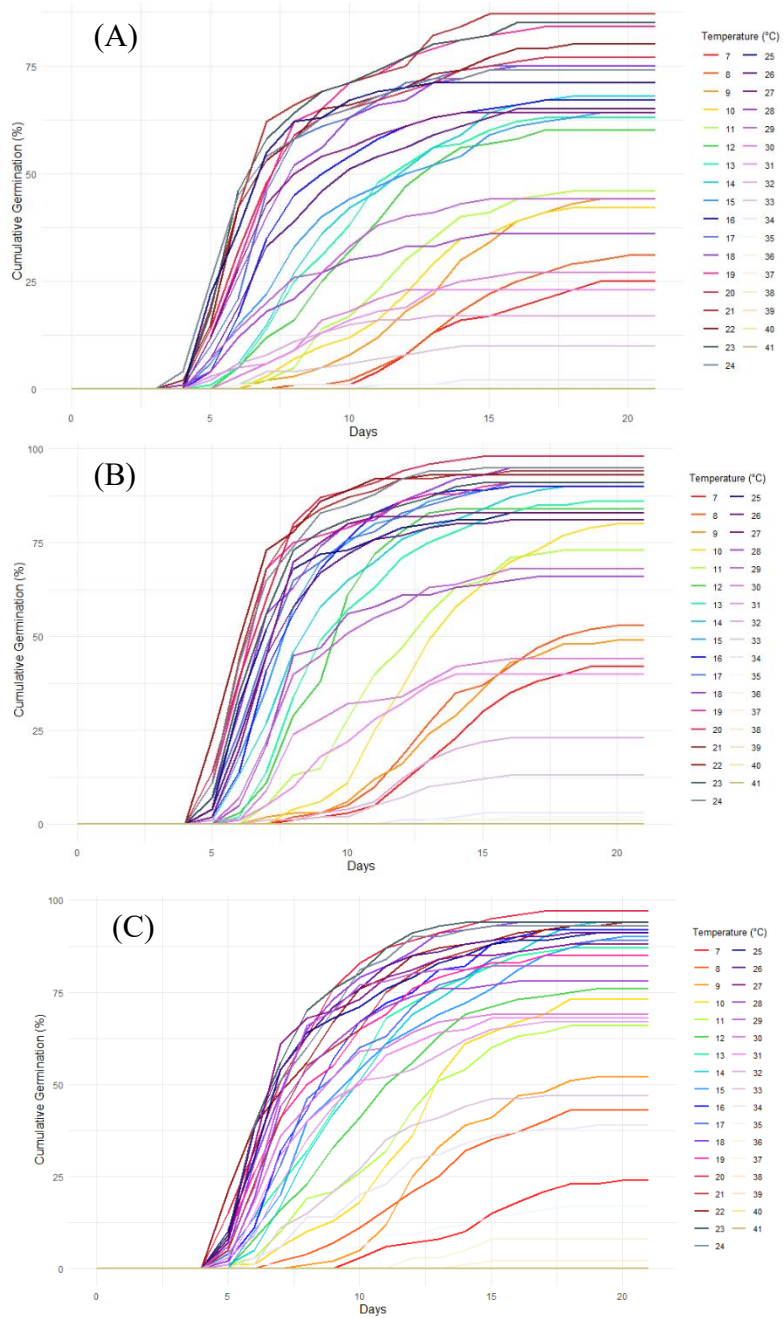


Figure 4.3 Cumulative germination percentage of (A) wild carrot (B) male lines (C) female lines of cultivated carrot seeds across a temperature gradient from 7 - 41 °C

4.3.2 Determining threshold germination temperatures by using regression models

Identifying the threshold germination temperature is vital for understating the germination patterns of seeds, as it helps in determining the minimal/base (T_b), maximal/ceiling (T_c), and optimal temperatures (T_o) for their survival (Adam et al., 2007). It has been demonstrated in previous studies that nonlinear models accurately captured the curvilinear relationship between the germination rate and temperature closer to the optimal value than linear models (Catara et al., 2016; Masin et al., 2017). In this study, nonlinear models outperformed the linear broken-stick model (**Figure 4.4**), as indicated by higher R^2 values and better overall fit, as shown in **Figure 4.5**. Therefore, three different nonlinear models, viz., polynomial, exponential, and hyperbolic models, were used in this study to assess the threshold germination temperature of wild carrots and cultivated carrots, including male and female lines. Models fitted to GR₅₀ vs temperature gradient (7 °C - 41 °C) for wild carrots, and male and female lines of cultivated carrots are presented in **Figure 4.5**, whereas the threshold germination temperature estimated by different models, along with model statistics are shown in **Table 4.4**.

Among the three models, the most accurate experimental model was selected based on the highest R^2 values and lower values of $RMSE$ and AIC to assess the threshold germination temperatures. The highest R^2 values and the lowest values of $RMSE$ and AIC were obtained with exponential models were used to compare temperature and seed germination rates of wild carrots (R^2 : 0.859, $RMSE$: 0.021, and AIC : -161.69), and male lines (R^2 : 0.969, $RMSE$: 0.009, and AIC : -219.52) and female lines (R^2 : 0.975, $RMSE$: 0.008, and AIC : -226.69) of cultivated carrots (**Table 4.4**). Based on these statistical criteria, it is evident that the exponential model, as compared to the polynomial and hyperbolic models, is the most appropriate experimental model for estimating and modelling the threshold temperatures of both wild and cultivated carrots. Consequently, the exponential model was used to obtain cardinal threshold temperatures for wild and cultivated carrots. Moreover, these findings support the observation

made by Cabrera-Santos et al. (2022), who reported that the exponential (beta) models (R^2 : 0.99, $RMSE$: 0.22) have best explained the response of *Salvia hispanica* seed germination (50th percentile) to temperature than segmented models (R^2 : 0.83, $RMSE$: 0.22). Generally, segmented models are used to demonstrate the relationship between germination rate and temperature with distinct sub-optimal and supra-optimal phases. Similar findings have been reported by Masin et al. (2017), who modelled the germination rate of weed species *Senecio vulgaris* L., *Sonchus oleraceus* L., and *Taraxacum officinale* W., with constant and alternative temperatures using the broken-stick model (linear model) and the exponential model, obtaining lower $RMSE$ and AIC values from the exponential model than the broken-stick model. Based on these, it is clear that the exponential model is beneficial in predicting cardinal temperatures in response to seed germination rates due to its flexibility in handling nonsymmetric responses, especially when a realistic exponential relationship exists between germination rate and temperature (Cabrera-Santos et al., 2022; Catara et al., 2016).

Assessing cardinal temperatures, including base, optimum, and ceiling temperature, is important for determining seed germination, as these identify the temperature limits for seed germination (Kamkar et al., 2012). Furthermore, cardinal temperature differs with genotypes since different genetic traits influence a seed's ability to withstand and react to temperature extremes, affecting germination patterns across different environmental conditions (Andreucci et al., 2016), which emphasises the importance of understanding the cardinal temperature of different genotypes of carrots (wild and cultivated carrots). Base temperatures (T_b), about which seed germination can be initiated, varied among the studied carrot genotypes, with estimates of 1.18 °C for wild carrots, 2.98 °C for male lines, and -0.22 °C for female lines of cultivated carrots (**Table 4.4**). Moreover, McCormick et al. (2014) reported that the T_b requirement of Hybrid carrot No 31 under New Zealand conditions was 0.1 °C, which lay in between -0.22 °C and 2.98 °C (**Table 4.4**) of T_b obtained from the present study. This is

consistent with results obtained by Finch-Savage et al. (1998), who found the T_b of 2.15 °C from carrot cultivar ‘Nandor’ in the UK. These findings clearly indicated that T_b for germination can vary substantially among the carrot genotypes. This variability reflects the specific genetic makeup of each genotype, which impacts their thermal requirements for germination.

Understanding the requirement of optimum temperature (T_o) for carrot seed germination is important for identifying optimal environmental conditions during the sowing period, as it ensures favourable conditions for seed germination and seedling emergence while implementing weed management strategies to control wild carrots. The optimum temperature was estimated for wild carrots, male lines, and female lines of cultivated carrots using exponential models as 23.8 °C, 22.1 °C, and 25.6 °C, respectively (**Table 4.4** and **Figure 4.5**). These T_o values are lower than those reported by McCormick et al. (2014) for the hybrid carrot seed germination (30.9 °C), who have used a segmented model (dent-like model) for the estimation of cardinal temperature, which might be one of the key reasons for the observed variation in T_o . Hence, it is important to select an appropriate modelling approach when evaluating the cardinal temperatures by considering relevant model statistics. On the contrary, Pereira et al. (2008) stated that the optimum temperature for the germination of carrot cv. Brasília is 20 °C, which is slightly lower than the result from this study (22.11 °C to 25.55 °C). Similarly, Corbineau et al. (1994) investigated the impact of temperature on seed germination across 8 different carrot cv, Almaro, Anglia, Duke, Nandor, Nantucket, Tancar, Tardia, and Valor, and noted that the thermal optimum for these cultivars ranged from 25 °C to 30 °C. The differences in T_o for the germination of carrot seed can be attributed to variations among carrot genotypes, as each genotype has particular threshold temperatures that affect its efficiency of germination, as well as to environmental conditions during seed maturation, which can affect the temperature sensitivity of different seed lots.

Furthermore, the estimated ceiling temperatures (T_c) for seed germination were 37.88 °C for wild carrot, 38.07 °C for carrot male lines, and 38.64 °C for carrot female lines (**Table 4.4** and **Figure 4.5**). According to McCormick et al. (2014), the T_c for seed germination of Hybrid carrot No 31 was 40.7 °C, which is slightly higher than the findings of this study (37.88 °C to 38.64 °C). These findings can be further supported by Corbineau et al. (1995) and Pereira et al. (2007), who reported that the germination capacity of carrot seed declines significantly when the temperature exceeds 30 °C, and it can be completely inhibited in the range of 40 °C to 45 °C. Furthermore, exceeding this range results in damage to the embryo or complete cell death (Lippmann et al., 2019). Due to the biennial behaviour of the carrot seed crop, it is vital to achieve high seed germination during their early first year to ensure successful flowering and seed production in the second year (Goodger, 2013). Hence, it is important to identify the requirements of cardinal temperatures (T_b , T_o , and T_c) for seed germination, particularly when using male and female lines for hybrid carrot seed production. Moreover, assessing the cardinal temperature requirement of both male and female carrot lines confirms that their germination and subsequent phenological stages are synchronized, which is important for effective pollination in hybrid seed production (Broussard et al., 2017). The findings of this study can be used to precisely predict the planting schedule under different climatic conditions. Understanding how environmental conditions affect germination can help to identify the optimal time for seed sowing, which is important to optimize crop establishment and growth. For instance, knowing the temperatures at which germination rates are highest allows growers to plan planting around optimal conditions for seedling survival and growth. This also facilitates to minimise the risk of planting too early or too late, ensuring higher success rates in seedling establishment. Similar studies have been carried out to optimize the sowing dates of various crops, such as corn in Iran (Edalat & Kazemeini, 2014), wheat in North China Plain (Wu et al., 2017), oats in Mongolia (Zhang et al., 2019), temperature pasture species in New

Zealand (Moot et al., 2000), which further highlight the importance of using cardinal temperatures to determine the optimal time for sowing of carrot seeds as well.

Understanding the cardinal temperature requirement for the seed germination of wild carrots is vital in formulating effective weed management strategies (Marschner et al., 2024). For instance, the low base temperature of wild carrots at 1.18 °C indicates that the wild carrots can germinate year around, giving them competitive advantages over carrot seed crops. This can increase the possibility of coinciding flowering of wild and cultivated carrots, which contaminate the purity of commercial seed production via undesirable pollen flow from wild to cultivated carrots (Magnussen & Hauser, 2007). Therefore, it is important to implement weed management strategies to control wild carrots, such as monitoring seedling emergence and application of herbicides during the time of germination and early emergence, throughout the year (Aulakh, 2020; Bradley et al., 2004; Soltani et al., 2017; Stachler & Kells, 1997).

The T_o of wild carrots (23.83 °C) is higher than the temperature of autumn and spring months in Hawke's Bay (autumn: 14.92 °C and spring: 14.22 °C) and Canterbury regions (autumn: 12.42 °C and spring: 11.75 °C) (<https://cliflo.niwa.co.nz>). This means seed germination of wild carrots can occur in the months of spring and leading to synchronization of flowering with cultivated carrots (Mandel & Brunet, 2019). However, the spring and autumn temperatures of Hawke's Bay and Canterbury fall within the sub-optimal temperature range (1.18 °C - 23.83 °C), creating favourable conditions for the establishment of wild carrots in these regions. These facts indicate the importance of timely management of wild carrots in these major carrot seed-producing regions (Godwin et al., 2024a). Furthermore, the T_c of wild carrots at 37.88 °C, indicates an upper limit for their germination and survival. The T_c range of wild carrots varies similarly to that of other weed species, including *Conyza bonariensis*, (31.5 °C – 34 °C) *Papaver dubium* (39.6 °C), *Papaver rhoeas* (39.1 °C) (Golmohammadzadeh et al., 2022; Valencia-

Gredilla et al., 2020). This temperature threshold is critical to the seasonal survival and infestation of wild carrots, specifically in warmer climates.

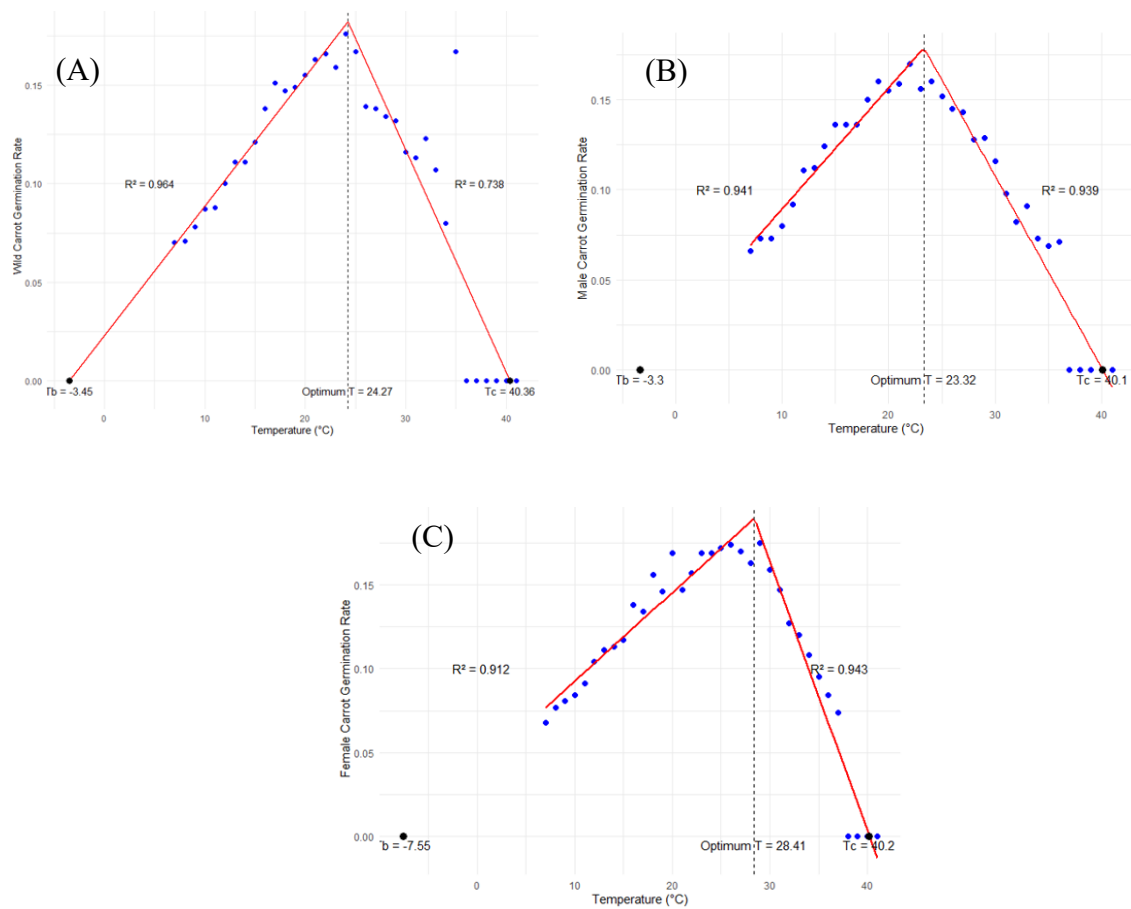


Figure 4.4 Threshold germination temperatures and model statistics of (A) wild and (B) male and (C) female lines of cultivated carrots estimated from linear (broken-stick) model

Table 4.4 Threshold germination temperatures and model statistics of wild and cultivated carrots, as estimated from three different nonlinear models

Genotype	Model	Cardinal temperature			Thermal time (°C days)	Model statistics		
		T_b (°C)	T_o (°C)	T_c (°C)		R^2	$RMSE$	AIC
Wild carrot	Polynomial	4.36	21.73	39.07	77.54	0.836	0.022	-158.54
	Exponential	1.18	23.83	37.88	111.74	0.859	0.021	-161.69
	Hyperbolic	-3.81	25.55	36.99	158.9	0.852	0.021	-160.19
Male line	Polynomial	4.08	21.44	38.49	79.64	0.966	0.01	-218.08
(Cultivated carrot)	Exponential	2.98	22.11	38.07	92.31	0.969	0.009	-219.52
	Hyperbolic	-2.09	23.83	37.21	139.80	0.943	0.012	-198.56
Female line	Polynomial	4.75	22.58	40.41	74.93	0.913	0.015	-184.44
(Cultivated carrot)	Exponential	-0.22	25.55	38.64	125.51	0.975	0.008	-226.69
	Hyperbolic	-4.25	27.26	37.99	162.46	0.958	0.011	-208.38

Note: T_b , base temperature; T_o , optimum temperature; T_c , ceiling temperature; R^2 , coefficient of determination of the regression; $RMSE$, root mean square error; AIC , Akaike information criterion

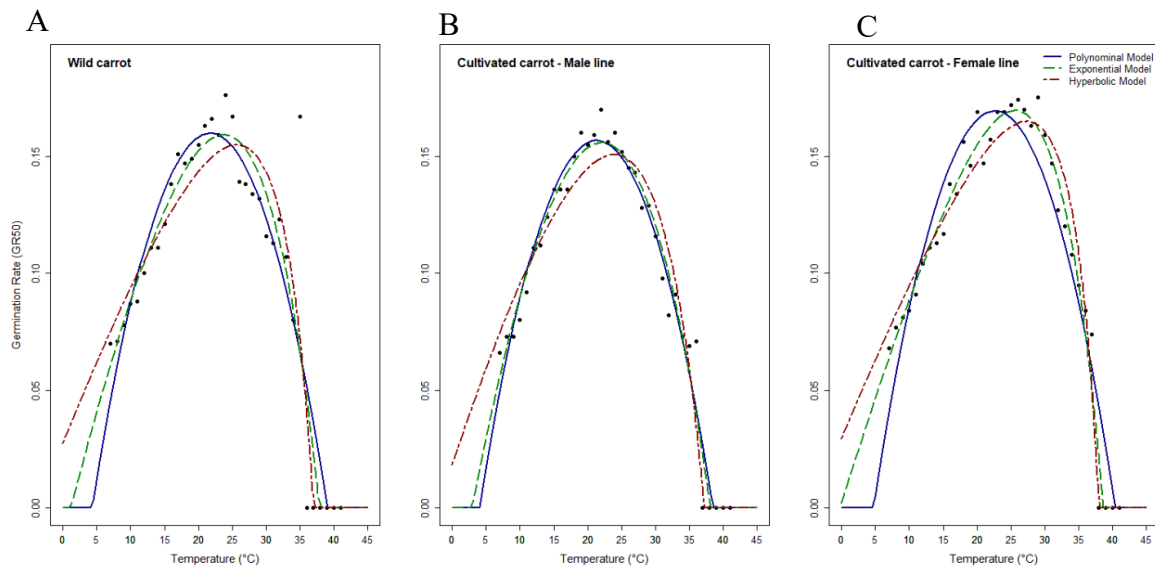


Figure 4.5 Projected (lines) vs observed (symbols) germination rates of wild carrots (A) and, male (B) and female lines (C) of cultivated carrots across the temperature gradient using different nonlinear models

4.3.3 Impact of projected climate change on seed germination of wild and cultivated carrots

According to the NIWA's (National Institute of Water and Atmospheric Research) climate change projections, temperatures are predicted to increase under RCP 2.6, 4.5, and 8.5 compared with the baseline period (1971-2005) during the carrot seed sowing season (autumn), and wild carrot establishment seasons (autumn, and spring) in the major carrot seed producing regions (Canterbury and Hawke's Bay regions) in New Zealand (**Figure 4.6**). As shown in **Figure 4.6**, the baseline average temperature during the carrot seed germination and wild carrot establishment phase (autumn) in Hawke's Bay and Canterbury regions are 14.30 °C and 12.32 °C, respectively. The baseline temperatures for the spring season, where wild carrots are established as summer annual, are 13.57 °C for the Hawke's Bay region and 12.22 °C for the Canterbury region. Furthermore, temperature is likely to increase more with higher radiative

forcing RCPs (**Figure 4.6**) since they denote higher greenhouse gas concentrations in the atmosphere leading to more heat being trapped, and stronger global warming (Adak et al., 2023). Similarly, Jalali et al. (2023) reported that, by 2090, the temperature rise in New Zealand would be comparatively greater under RCP 8.5 than RCP 4.5. Moreover, variations in autumn temperature, compared with the baseline period 1971-2005, are higher under RCP 4.5 and RCP 8.5 in the Canterbury region than in the Hawke's Bay region (**Figure 4.6, and Table 4.5**). The autumn temperature is important for the seed germination and seedling establishment of cultivated carrots (Godwin et al., 2023). Therefore, it is beneficial to expand the carrot seed production in Hawke's Bay region in the context of projected climate change (Bhatia, 2023).

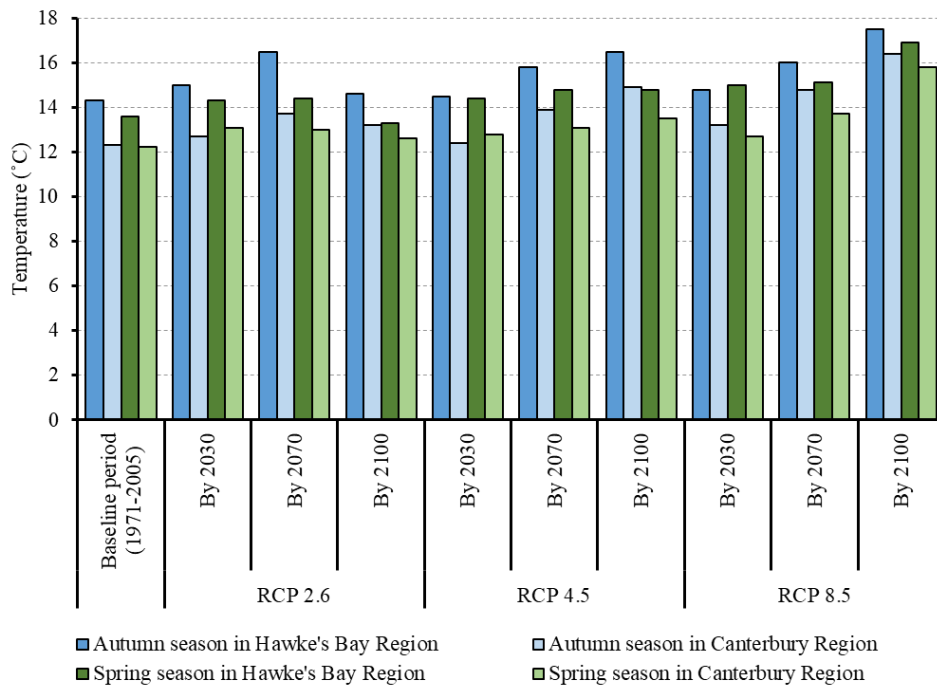


Figure 4.6 Temperature projections for carrot seed sowing season and wild carrot establishment seasons in Canterbury and Hawke's Bay regions, New Zealand

The results showed that the GR₅₀ of wild and cultivated carrots, including male and female lines will increase with increasing temperature in Canterbury and Hawke's Bay region under projected climate change conditions (**Table 4.5 and Table 4.6**). The highest percentage of increase in projected GR₅₀ by 2100 is reported in the Canterbury region under RCP 8.5, with

26.37 % for wild carrots, 25.67 % for male lines, and 26.88 % for female lines of cultivated carrots (**Table 4.5**). The increase in GR₅₀ for wild and cultivated carrots, including male and female lines, is attributed to the projected temperatures falling within the sub-optimal range, between the T_b and T_o , which enhances GR₅₀ under climate change conditions in the Canterbury and Hawke's Bay regions. Similar findings were reported by Sousaraei et al. (2022), who stated that the increasing temperature, as a result of global warming, can result in rapid germination (higher GR₅₀) in different landraces of tomatoes in Iran. Moreover, Milbau et al. (2009) observed that the summer warming (+ 2.5 °C) has accelerated the germination of different trees (*Alnus incana*, and *Betula pubescens*), shrubs (*Betula nana*, and *Vaccinium myrtillus*) grass species (*Calamagrostis lapponica*, and *Festuca ovina*) in subarctic northern Sweden.

The increasing GR₅₀ of wild carrots, driven by the predicted increase in temperature, implies higher degree of infestation, ultimately resulting in a threat to carrot seed production via undesirable pollen flow from wild to cultivated carrots. Wild carrots can establish themselves as either winter annuals (germinating in autumn, overwintering during the winter, and flowering in summer) or summer annuals (established in spring, and flowering in summer). The findings of this study revealed that the GR₅₀ of wild carrots (winter annuals) is more favoured by the projected autumn temperature rises under the RCP 4.5 (except by 2030) and RCP 8.5 in the Canterbury region compared to the Hawke's Bay region (**Table 4.5**). The increase in predicted spring temperature in the Canterbury region has strongly influenced the GR₅₀ of wild carrots (summer annuals) under RCP 8.5 (except by 2030) compared with the Hawke's Bay region (**Table 4.6**). This indicates that seed germination of wild carrots is likely to accelerate more significantly in Canterbury under long-term and extreme climate change scenarios, such as RCP 8.5, possibly resulting in higher levels of wild carrot infestation and a greater effect on commercial carrot seed production. To alleviate the threat caused by the infestation of wild carrots due to projected temperature increments, it may be necessary to shift

and expand the carrot seed production to other regions, such as Hawke's Bay region (Bhatia, 2023).

Table 4.5 Climate change scenario and its effect on seasonal mean temperature (autumn) changes (°C) and Percentage (%) of variation in projected GR₅₀ of wild and cultivated carrots

Climate change scenario	Projected year	Changes in mean autumn temperature (°C)		Percentage (%) of variation in projected GR ₅₀					
		Hawke's Bay	Canterbury	Hawke's Bay			Canterbury		
				Wild carrot	Cultivated carrot		Wild carrot	Cultivated carrot	
					Male line	Femal e line		Male line	Femal e line
RCP 2.6	By 2030	0.70	0.38	3.90	3.77	4.05	2.80	2.86	2.73
	By 2070	2.20	1.38	11.54	10.68	12.24	9.79	10.02	9.59
	By 2100	0.30	0.88	1.70	1.65	1.74	6.34	6.53	6.20
RCP 4.5	By 2030	0.20	0.08	1.14	1.10	1.16	0.65	0.63	0.56
	By 2070	1.50	1.58	8.10	7.61	8.52	11.18	11.36	11.00
	By 2100	2.20	2.58	11.54	10.68	12.24	17.61	17.62	17.58
RCP 8.5	By 2030	0.50	0.88	2.81	2.67	2.89	6.34	6.53	6.20
	By 2070	1.70	2.48	9.11	8.56	9.59	16.96	16.99	16.92
	By 2100	3.20	4.08	16.03	14.44	17.29	26.37	25.67	26.88

Table 4.6 Climate change scenario and its effect on seasonal temperature (spring) changes (°C) and Percentage (%) of variation in projected GR₅₀ of wild carrots (summer annuals)

Climate change scenario	Projected year	Changes in mean spring temperature (°C)		Percentage (%) of variation in projected GR ₅₀	
		Hawke's Bay	Canterbury	Hawke's Bay	Canterbury
RCP 2.6	By 2030	0.73	0.88	4.45	6.38
	By 2070	0.83	0.78	5.05	5.63
	By 2100	-0.27	0.38	-1.71	2.72
RCP 4.5	By 2030	0.83	0.58	5.05	4.22
	By 2070	1.23	0.88	7.36	6.38
	By 2100	1.23	1.28	7.36	9.19
RCP 8.5	By 2030	1.43	0.48	8.55	3.47
	By 2070	1.53	1.48	9.07	10.51
	By 2100	3.33	3.58	18.48	23.83

4.4 Conclusion

The key objectives of this study were, to determine the impacts of temperature gradient on seed germination of wild and cultivated carrots (including male and female lines), to estimate the cardinal temperature using different threshold models, and to relate it with predicted climate change in major seed-producing regions in New Zealand. According to the ANOVA results, it is evident that the temperature, genotypes, and their interactions have significantly ($p < 0.05$) affected the germination percentage, mean germination time, and time required for 50 % germination of different carrot genotypes. The highest percentage of germination was reported at temperatures of 20 °C for cultivated carrots, including male (98 %) and female (97 %) lines,

and 21 °C for wild carrots (87 %). Furthermore, seed germination was completely inhibited at temperatures above 35 °C for wild carrots, 36 °C for the male line, and 37 °C for the female line. The lowest MGT was noted at temperatures of 25 °C for wild carrots (6.8 days), 22 °C for male lines (6.7 days), and 23 °C for female lines (6.6 days) within the temperature range of 7 °C - 31 °C. Meanwhile, the lowest T_{50} was observed at temperatures of 24 °C for wild carrots (5.7 days), 22 °C for male lines (5.9 days), and 29 °C for female lines (5.7 days). The study confirmed that the current sowing time is advantageous for the seed germination of male and female lines of cultivated carrots in carrot seed-producing regions in New Zealand. Although three different threshold models were studied for calculating GR_{50} , the exponential model was selected based on statistical criteria, such as higher R^2 , and lower $RMSE$ and AIC values, for the estimation of base (T_b), optimal (T_o), and ceiling (T_c) temperature requirement for the seed germination of male and female lines of cultivated carrots, and wild carrots. The lowest T_b and the highest T_c were estimated in female lines of cultivated carrots as -0.22 °C, and 38.64 °C, respectively. The T_o of studied carrot genotypes ranged from 22.11 °C to 25.55 °C. Climate change projection in Hawke's Bay and Canterbury regions of New Zealand revealed that the GR_{50} of wild and cultivated carrots, including male and female lines will increase with increasing temperature. The highest percentage of rise in projected GR_{50} by 2100 is estimated in the Canterbury region under RCP 8.5, with 26.37 % for wild carrots, 25.67 % for male lines, and 26.88 % for female lines of cultivated carrots. As a result of temperature increment, driven by climate change projections, the infestation of wild carrots may increase as a result of the increasing GR_{50} of wild carrots, which is more important for successful emergence and establishment. This can affect carrot seed production via unwanted pollen flow from wild to cultivated carrots. Therefore, carrot seed production regions should be expanded to comparatively more climatically favourable locations with comparatively lower wild carrot infestation, such as Hawke's Bay, to produce high-quality commercial carrot seeds. To support

this, a systematic survey should be conducted to identify wild carrot-free sites within the Hawke's Bay region suitable for commercial seed production. The findings of this study provide important insights for stakeholders, researchers, industries and growers to develop and incorporate climate-resilient commercial carrot varieties in cultivation, formulate weed management plans to minimize the wild carrot infestation, shift and expand carrot seed growing regions to ideal locations, and make appropriate decisions for the improvement of carrot seed production. In conclusion, these findings significantly advance our current knowledge of the seed germination behaviour of cultivated and wild carrots, particularly in the context of their cardinal temperature requirements. Finally, we would like to highlight that this study is the first report of cardinal temperature determination of wild and cultivated carrots, including male and female lines; our data for the T_b , T_o , and T_c for wild and cultivated carrot seed germination provide basic temperature requirements that can be incorporated in future research and cropping of cultivated carrots and weed management of wild carrots.

Chapter 5: Comparing vegetative growth patterns of cultivated and wild carrots to eliminate genetic contamination from weed to crop

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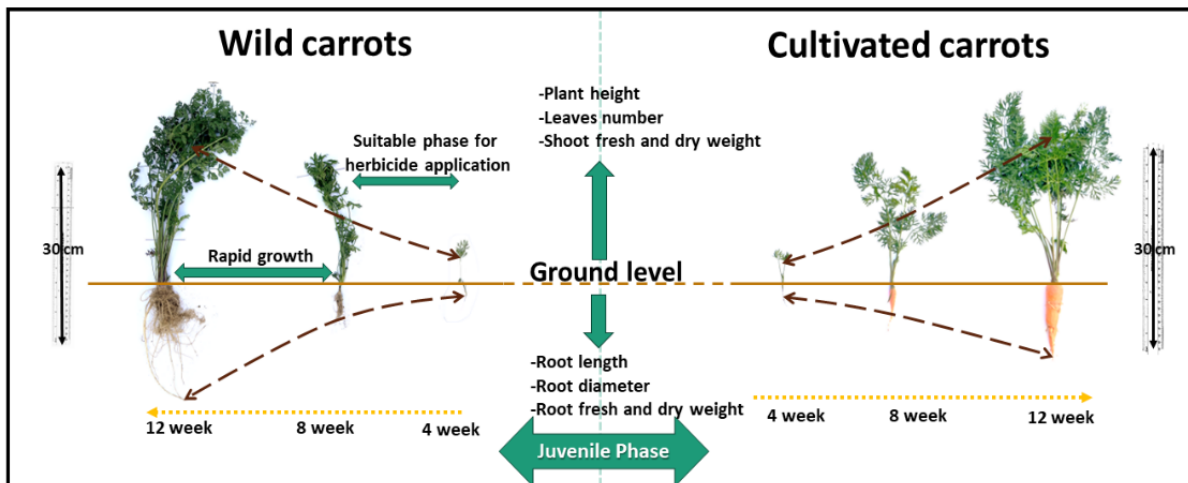
*Citation: **Godwin, A., Pieralli, S., Sofkova-Bobcheva, S., Ward, A., & McGill, C. (2024).***

*Comparing vegetative growth patterns of cultivated (*Daucus carota* L. subsp. *sativus*) and wild carrots (*Daucus carota* L. subsp. *carota*) to eliminate genetic contamination from weed to crop.*

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The literature review in Chapter 2 (2.2) demonstrated that wild carrots must be controlled prior to flowering to avoid the proliferation of seeds. Moreover, chapter 4 indicated that the germination percentage and rate of wild carrots is likely to increase under changing climatic conditions. Therefore, it is highly important to find out which growth phase is optimum to control the wild carrots in the context of weed management strategies. However, no studies have compared and modelled the vegetative growth patterns of wild and cultivated carrots in the context of wild carrot management, specifically in New Zealand. Accordingly, the objective of chapter 5 is to compare the different morphological traits of wild and cultivated carrots at three different vegetative stages (4 weeks, 8 weeks, and 12 weeks), as well as predict the ideal wild carrot growth stage at which to execute the weed management practices to control the wild carrots adjacent to the carrot seed-growing sites.

Graphical abstract



Abstract

Wild carrot is a problematic weed that can threaten the genetic purity of cultivated carrots by hybridization. Wild carrots must be controlled before flowering to avoid undesirable crossing with cultivated carrots. Understanding wild carrot's vegetative growth pattern helps formulate sustainable weed management practices. However, little is known about the vegetative growth patterns of wild and cultivated carrots. A pot experiment was carried out to compare and model the vegetative growth pattern of different morphological traits in both wild and cultivated carrots. This study was executed in a glasshouse located in Palmerston North, New Zealand. A factorial randomized complete block design (RCBD) with two factors and four replications was used. The first factor was assigned to the carrot genotype (cultivated and wild) and the second factor to length of juvenile stages (12-weeks, 8-weeks, and 4-weeks). Plant height, leaf number, shoot fresh and dry weight, root fresh and dry weight, root diameter and root length were measured. Data were analysed using analysis of variance (ANOVA), principal component analysis (PCA), correlation, and regression analysis. At the 8-week juvenile stage (9-11 leaves stage), wild carrot's shoot and root characteristics exhibited rapid growth. Correlation analysis indicated positive and significant ($p < 0.05$) correlations between above and below-ground

morphological traits. PCA showed that morphological characteristics, except plant height, can be used to distinguish wild and cultivated carrots. To predict the vegetative growth pattern of most of the morphological traits of wild and cultivated carrots, power regression models were selected based on higher R^2 and $adj-R^2$ values and lower values of $RMSE$, AIC and BIC . The study showed wild carrots grew more quickly than cultivated carrots during the vegetative phase. It is recommended that appropriate weed management practices, such as hoeing, tilling, hand pulling, or herbicide spraying, be implemented before wild carrot leaf stages 9–11.

Keywords: Morphological trait, Carrot seed production, Vegetative growth, Weed management, Wild carrot

5.1. Introduction

Weed infestation is one of the key factors restricting crop production globally (Mayerová et al., 2018). Approximately, 31.5 % of the yield loss is caused by about 1800 weed species resulting in annual economic losses of USD 32 billion (Kubiak et al., 2022). Numerous region-specific and local abiotic, biotic, and anthropogenic factors have an impact on weed infestations (Meyer et al., 2021; Otieno et al., 2022). On a global scale, weeds and invasive alien plants have generated issues in agroecosystems as a result of changes in their geographical distribution and population densities (Marambe & Wijesundara, 2021). Due to the significant spatiotemporal variability and genetic diversity of the weed population, identifying the specific variables linked to effective weed management is important (Gafni et al., 2023).

Carrot (*Daucus carota* L. subsp. *sativus*) is a member of the family Apiaceae. It is a widely consumed vegetable due to its high nutritional characteristics, especially vitamin A (Junaid et al., 2023; Olmedilla-Alonso et al., 2020). As a result, the consumption of carrots and related products has expanded gradually (Singh et al., 2021). In the United States, per capita consumption of carrots has increased over the last century, rising from 2.2 pounds (~1 kg) in

1919 to an estimated 8.8 pounds (~4 kg) in 2022 (USDA, 2022). Hence, global demand for carrots is climbing, generating an increased market for carrot producers and a consequent requirement for carrot seeds (Simon, 2019b). Although farm inputs such as fertilizers, pesticides, and herbicides are important to enhance carrot productivity, genetically superior seeds are essential inputs for the establishment of plants and transfer of desirable traits to subsequent offspring (Njonjo et al., 2019). Therefore, the production of genetically pure carrot seeds needs to be guaranteed to meet the quality requirements of carrot root producers, where the seed is the only planting material used to propagate and establish carrot seedlings (Chaitra et al., 2018).

The production of high-quality carrot seeds is influenced by the temperate climate, where long days are necessary for seed formation during all growth phases, with the exception of vernalization (Wohlfeiler et al., 2021). Vernalization, which happens throughout the winter months (low temperature under short-day conditions), induces the transition from the vegetative phase to the reproductive phase of carrot seed crops (Godwin et al., 2023). The growth phase of carrots prior to the low-temperature vernalization is known as juvenility. This phase generally ends after reaching the 8-12 leaves stage, which can be reached by 12 weeks from seed sowing. Due to this, the present study consists of different lengths of juvenile phases with a maximum of 12 weeks (Linke et al., 2019). Carrot seeds are mainly produced from open-pollinated and hybrid seed crops worldwide (Simon, 2021), and the hybrid carrot seed crop sector is expanding in New Zealand for the production of genetically pure carrot seeds (Bhatia, 2023). In hybrid carrot seed production, male fertile lines and male sterile lines, generally known as cytoplasmic male sterile lines (CMS), serve as pollen donors (paternal parent) and pollen receptors (maternal parent), respectively (Linke et al., 2019). Insect pollinators, such as honeybees (*Apis mellifera* L.), Calliphorid flies (*Calliphora vicina*), nectar scarabs, and hoverflies (*Eristalis tenax*) facilitate the transfer of pollen to the receptive stigmas (Ali et al.,

2022; Gaffney et al., 2018). Such a pollen distribution mechanism makes it possible for unwanted pollen to flow from carrot cultivars with undesirable features as well as wild carrots (Mandel & Brunet, 2019).

Wild carrot (*Daucus carota* L. subsp. *carota*) also belongs to the Apiaceae family. Wild carrot is often referred to as Queen Anne's lace and is considered a serious weed in several parts of the world (Muturi et al., 2019). Studies have indicated that European colonization was one of the reasons for the dispersal of wild carrots across the globe (Iorizzo et al., 2013). Depending on the geographical location and climatic conditions, wild carrots can exhibit annual, biennial or perennial growth habits (Mandel & Brunet, 2019). Moreover, previous literature indicated that wild carrots grow in open habitats, especially in wastelands and roadsides (de Jong et al., 2016). Furthermore, wild carrots appear to be adaptable to a wide range of soil conditions (Praciak, 2015) and can sustain themselves in challenging soil conditions (Mezghani et al., 2019). Since the cultivated carrot and wild carrot are sexually compatible relatives, hybridization is possible between wild and cultivated carrots. Furthermore, a broad variety of insect species from 15 different families are attracted to the wild carrot flowers. The same pollinators may also forage flowers of cultivated carrots. During the pollination process, wild and cultivated carrots can compete with one another to attract pollinators. As a result, pollen transmission from wild-type to cultivated carrot is feasible and reciprocal (Mandel & Brunet, 2019). However, gene flow from wild to cultivated carrots can negatively impact commercial carrot seed production, where the possibility of a loss of genetic purity can be expected in carrot seeds. A commercial carrot seed line may be unsaleable in the target market if it contains characteristics of wild type (Ellstrand et al., 2013; Rong et al., 2010). Genetically impure seed lots are often identified by the presence of early bolters in cultivated fields when hybrids between crop and wild plants flower early, yielding less edible, white-rooted carrots (Greibenstein et al., 2013; Mandel et al., 2016). To avoid undesirable hybridization, a 1 to 2

mile (1.6 km to 3.2 km) isolation distance from wild carrots should be maintained during commercial carrot seed production (Bhardwaj et al., 2020). However, crop-weed hybridization continues to be a significant issue thus deteriorating the genetic purity of cultivated carrot seeds (Mandel et al., 2016). Furthermore, the local commercial carrot seed industries are under constraint, particularly for expansion, due to the dramatic increase in the spread of wild carrots in carrot seed-producing regions, including New Zealand and the United States, over the past few years (Bhatia, 2023; Rome & Lucero, 2019). Based on discussions with South Pacific Seeds in New Zealand, wild carrots are emerging as a significant problem for carrot seed growers, posing challenges for seed purity (Richard van Garderen, South Pacific Seeds (NZ) Ltd., personal communication, 2024). To minimize outcrossing and seed rain, wild carrots need to be controlled before flowering. It is therefore important to understand the vegetative growth pattern of wild carrots to enable the implementation of weed management strategies. From a breeding point of view, the introgression is advantageous, where the beneficial characteristics of wild carrots, such as environmental adaptability, disease resistance, and abiotic stress tolerance, can be introduced into cultivated carrots via breeding programmes (Rong et al., 2010; Simon et al., 2021).

Understanding the morphological characteristics of weed species by evaluating their growth patterns assists in developing weed management strategies prior to the critical period of weed control (Alagbo et al., 2022; Dille, 2014). In agriculture, growth curves are widely utilized as a tool to analyze and simulate how plants grow over time and in response to certain climatic circumstances (Cheriere et al., 2023; León-Burgos et al., 2022). Generally, growth models are developed based on mathematical functions through various regression analyses, such as linear, non-linear and probit analysis (Bakhshandeh et al., 2020). Consequently, several statistical criteria, including the coefficient of determination (R^2), adjusted coefficient of determination ($adj R^2$), root mean square error ($RMSE$), Akaike Information Criteria (AIC), and Bayesian

information criterion (*BIC*), can be used to find satisfactory growth curve fitting (Li et al., 2022; Tyasi et al., 2022).

Although many studies have examined the growth pattern of cultivated carrots, there are no studies that compared and modelled the growth pattern of wild and cultivated carrots together in the context of controlling wild carrots, particularly in New Zealand. This is a significant research gap in the existing scientific literature relevant to the management of wild carrots for the production of quality commercial carrot seeds. Integrating data on wild carrot phenology and weed biology can significantly enhance wild carrot control strategies. In this study, we aimed to compare the various morphological traits of wild and cultivated carrots at different vegetative stages (4 weeks, 8 weeks, and 12 weeks), as well as predict the optimal wild carrot growth stage at which to implement the essential weed management practices to control the wild carrots near the carrot seed-growing sites. Furthermore, determining the relationship between the above and below-ground morphological traits of wild and cultivated carrots makes it easier to understand how both plants' root systems grow without having to uproot them. To make inferences, various statistical methods were used including ANOVA (analysis of variance), PCA (principal component analysis), regression analysis, and correlation. The findings from this study facilitate the timely management of wild carrots, especially before flowering, which helps to produce genetically pure commercial carrot seeds through the prevention of undesirable pollen flow from wild to cultivated carrots. Additionally, the descriptive results on morphological characteristics obtained from this research could be used to formulate crop simulation models for both wild and cultivated carrots in future.

5.2. Material and methods

5.2.1. Experiment location

The study was conducted in a glasshouse at the Plant Growth Unit, Massey University, Palmerston North, New Zealand (40°22'40.9"S 175°36'49.1" E), from 26th July to 16th October 2022. The dimensions of the glasshouse were 15 m (length) and 6 m (width), with heights of 3.5 m and 1.7 m at the highest and lowest points. The daily air temperature was recorded with an electronic DS1923 temperature logger (iButton[®]) throughout the study period (**Figure 5.1**). The average, maximum and minimum temperatures were 20.25 °C, 25.62 °C and 16.44 °C, respectively. Depending on the temperature within the glasshouse, the windows automatically opened to allow fresh air to circulate. Day length was extended to provide long day conditions (18 hours light and 6 hours dark) to the carrot seedlings by using cool daylight fluorescent lights (Philips TLD 58w/865) in the glasshouse. Light metre (LI-COR; Model LI-250) measurements were used to determine the light intensity, which was maintained between 140 and 150 $\mu\text{mol m}^{-2}\text{s}^{-1}$ throughout the experiment (Wohlfeiler et al., 2021).

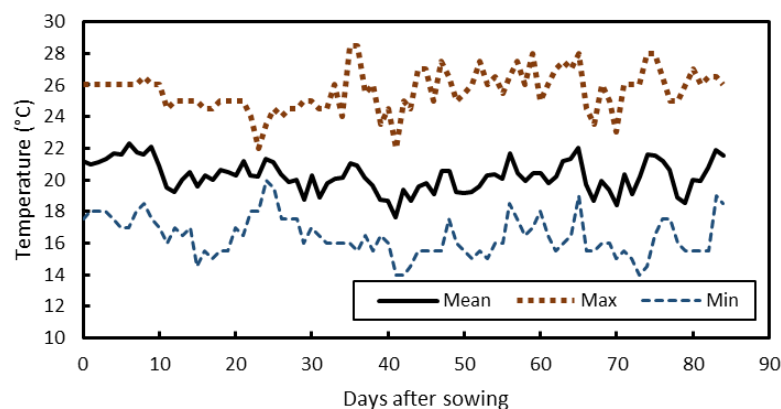


Figure 5.1 Temperature in the glasshouse during the study period

5.2.2. Planting materials, seedling establishment and crop husbandry

Both cultivated and wild carrots were grown in this study. Seeds of wild carrots were collected from Dairy One farm, Massey University in Palmerston North, New Zealand (40°22'31.0" S

175°36'21.3" E) in May 2022. Cultivated carrot seeds (No 27 Male lines) were sourced from South Pacific Seeds Ltd, New Zealand. PVC pipes (Marley OPTIM® DWV Pipe SN6) with a 10 cm diameter and a 50 cm height were filled with potting mixture and used to grow the plants from seed (Wohlfeiler et al., 2021). To improve the drainage of excess irrigation, garden nets were placed over the bottom of each pot. According to Yadav et al. (2021), the potting mixture used was prepared by mixing garden soil and sand in a 3:1 ratio with a concrete mixer. Subsequently, the pots were filled with 4 litres of potting mixture and 8–9 months slow-releasing fertilizer (Osmocot Exact Standard, 15N-3.9P-9.1K+1.2Mg+Trace elements) at the rate of 4 g/L. Cultivated and wild carrot seeds were sown on 26 July, 23 August, and 20 September 2022 to provide 12-week, 8-week and 4-week-old plants, respectively. Seeds were sown at a rate of 3 seeds per pot. A spray lance attached to the seedling nozzle was used for irrigation until seedling emergence. Following that, drippers were used to irrigate plants at the rate of 4 ml/day/plant throughout the experiment. Emerged seedlings were thinned to one plant per pot once they had three unfolded true leaves (Wohlfeiler et al., 2022). Over the entire duration of the study, manual weeding was done every week. Moreover, there were no pests and diseases observed during the experiment.

5.2.3. Treatment combinations and experimental design

The pot experiment was laid out according to a two-factor factorial arrangement in a randomized complete block design (RCBD) with four blocks per treatment. The two factors were carrot genotype (2 levels) and juvenile period of the carrot plant (3 levels), resulting in six treatment combinations (**Table 5.1**). Within each sowing date treatment block, plants were completely randomized. Each block comprised 9 pots per treatment combination (n=9). In total, 216 plants (6 treatment combinations × 4 blocks × 9 plants per block) were accommodated in the glasshouse.

Table 5.1 Factors and treatment combinations used in the experiment

Carrot Genotype	Juvenile stage (Date of sowing)	Combination of treatments
Cultivated (T₁)	12-week (26th July)- J ₁	T ₁ J ₁
	8-week (23rd August)- J ₂	T ₁ J ₂
	4-week (20th September)- J ₃	T ₁ J ₃
Wild (T₂)	12-week (26th July)- J ₁	T ₂ J ₁
	8-week (23rd August)- J ₂	T ₂ J ₂
	4-week (20th September)- J ₃	T ₂ J ₃

5.2.4. Sampling and measurements

All the plants were removed from their pots on October 16, 2022, in order to collect data on the quantitative morphological parameters at different growth stages (4, 8 and 12 weeks), such as fresh and dry weight of shoot (g), root length (cm), root diameter (mm) and fresh and dry weight of root (g). Prior to uprooting the samples, plant height (cm) was measured from the ground level to the top of the apex of the longest leaf using a measuring tape. While the number of leaves was determined by counting leaves from each sample (Agbede et al., 2017), root length was measured from the base to the top of the root by using a ruler (Daba et al., 2018). Root diameter was measured by using a digital 150 mm digital vernier caliper (Craftright, China) (Ghani et al., 2021). Fresh and dry weights of the shoots and roots were estimated using digital balances (Mettler Toledo PM 6100 Balance and Mettler Toledo AE100 Analytical Balance). After measuring the fresh weight, the root and shoot samples were separated and placed in paper bags to dry at 60 °C until reaching constant weight (Lumor et al., 2023).

5.2.5. Statistical analysis

Evaluation of both main and interaction effects between carrot genotype and juvenile stages of carrot seedlings was evaluated using a two-way analysis of variance (ANOVA) in the general linear model. Subsequently, a mean comparison was undertaken using Tukey's test at a 5 % significance level ($p < 0.05$). A Scree plot and eigenvalues (>1) were used for the selection of appropriate principal components (PCs) as a prerequisite to the PCA (Mukul, 2023). Thereafter, PCA biplot was plotted to distinguish the wild and cultivated carrots via clusters and to find out the importance of morphological traits in distinguishing the wild and cultivated carrots. Pearson correlation analyses were executed to study the relationship between the morphological traits of both wild and cultivated carrots, especially to compare the correlation between above and below-ground traits. To understand the growth pattern over time, four different models (linear, quadratic, log-linear and log-log) were evaluated using linear and nonlinear regression approaches. The exponential and power growth models were derived from log-linear and log-log functions, respectively. The acquired data from different morphological traits was randomly split into a training dataset (70 %) and a test dataset (30 %). The training and test datasets were used to calibrate and validate the selected models, respectively (Hudait & Patel, 2022). The following statistical criteria were applied to each mathematical function's adjustment and selection: coefficient of determination (R^2), adjusted coefficient of determination ($adj R^2$), root mean square error ($RMSE$), Akaike Information Criteria (AIC), and Bayesian information criterion (BIC). R studio (version 2022.07.2 + 576) was used for all statistical analyses.

5.3. Results and discussion

5.3.1. Effect of genotype and juvenile period on morphological traits

The results of the ANOVA and Tukey's test for the morphological traits of wild and cultivated carrots are shown in **Table 5.2** and **Table 5.3**, respectively. The interaction effect between genotype and juvenile period was significant ($p < 0.05$) for all morphological traits except plant height.

5.3.1.1. Plant height

In developing weed management strategies, weed height is an important deciding factor (Staver et al., 2020). There was no significant ($p > 0.05$) difference between the wild and cultivated carrots in terms of plant height if taken at the same juvenile stage, but there was a significant ($p < 0.05$) increase in plant height with increasing length of the juvenile period (**Table 5.3**). At the 12-week juvenile stage, the height of the cultivated and wild carrots was (38.05 ± 0.88 cm) and (35.95 ± 1.22 cm), respectively. When comparing plant heights of wild (25.1 – 33.9 cm) and commercial (31.6 cm) carrot populations from Norway, Sweden, and Denmark, the New Zealand wild and cultivated carrots have exhibited a higher growth rate (Solberg & Yndgaard, 2015). This demonstrates how the genotype of carrots, especially wild carrots, is different in terms of morphology all across the world (Mezghani et al., 2017). Furthermore, the plant height of cultivated and wild carrots has increased by 76.56 % and 76.77 %, respectively from 4 weeks to 12 weeks of juvenile stage. Relatively, the highest increment of plant height was 17.49 cm for wild carrots and 16.6 cm for cultivated carrots between 4 and 8 weeks after sowing. This highlights the significance of managing weeds in the early phases of growth; once they enter the rapid growth stage, wild carrots are extremely challenging to manage. Similar findings were made by Whitehead & Switzer (1963), who discovered that wild carrots can be completely controlled by using herbicides such as 2,4,5-T when they are between 15.24 cm -

20.32 cm (6-8 inches) in height. Meanwhile, Bradley et al. (2004) have revealed that several combinations of Picloram + 2,4-D and Triclopyr + clopyralid were effective in controlling the wild carrots at a height of 9 to 11 cm. Furthermore, Stachler & Kells (1997) used wild carrot plants with heights of 11–20 cm and 26–28 cm to compare the effectiveness of pre–emergence and post–emergence herbicides in a non–tillage soybean field in Michigan. Based on these findings, it is clear that the height of the wild carrot needs to be considered when recommending an herbicide. Furthermore, the size of the wild carrots grows along with plant height. Inconsistent weed control is commonly caused by improper herbicidal application due to the huge size of the weed at the time of spraying (Chauhan & Opeña, 2012; Jha et al., 2010). In order to boost the herbicidal efficacy, the rate of application could be increased to control the weeds. Therefore, it's important to control wild carrots as early as possible to minimize the cost of herbicide application.

5.3.1.2. Number of leaves

Leaf number is a significant morphological trait used to estimate the growth and development of plants (Kumar & Domnic, 2020) and to determine when to spray herbicides more effectively for weed management (Lu & Young, 2020; Weyler et al., 2021). The leaf number of wild carrots was significantly ($p < 0.05$) higher than the leaf count of cultivated carrots at all the juvenile stages. The highest leaf number was recorded as 25.00 ± 1.81 for wild carrots at 12 weeks after sowing, which was 67.08 % higher than the leaf number produced by cultivated carrots at the same growth stage (**Table 5.3**). Similarly, a previous study in the Netherlands showed that the wild carrot has produced approximately 54 % higher number of leaves compared with cultivated carrots at the 15-week juvenile stage (Greibenstein et al., 2013). Genetic variation is one of the influencing factors in the difference in leaf count in between wild and cultivated carrots (Wang et al., 2020). Furthermore, these findings support the statement made by Miao et al. (2021), who noted that different varieties of the same species could produce varying leaf

counts. Moreover, wild and cultivated carrots were shown to have a rapidly increasing trend in leaf counts between the 8 and 12 (by 14.66 leaves) weeks, during the 4 and 8 (by 3.79 leaves) weeks of the juvenile stage, respectively (**Table 5.3**). This indicates that the wild carrot needs to be controlled prior to the approximately 9 to 11 leaves stage (8 weeks of juvenile phase). Stachler et al. (2000) and Whitehead & Switzer (1963) found that using 5-14 leaf stages (average: 9.5 leaves) of wild carrots would be appropriate for the herbicidal efficacy studies. This is further supported by Colquhoun et al. (2003), who claimed that the application of an herbicide is successful while the wild carrot is at the seedling stage. Furthermore, determining the weed leaf number at different growth stages is beneficial for formulating weed management strategies, particularly for identifying the rate, time and type of herbicide application (Lati et al., 2019).

5.3.1.3. Shoot fresh and dry weight

Shoot fresh and dry weights are commonly used to study the growth pattern of plants (Jan et al., 2022). Larger weeds are more challenging to eradicate than small plants. Therefore, shoot fresh and dry weight should be taken into account when formulating weed management plans and researching their efficacy (Akbar et al., 2023; Cheng et al., 2021). Shoot fresh and dry weight of wild carrots at the 8 and 12-week juvenile stages were significantly ($p < 0.05$) higher than the cultivated carrots. The highest shoot fresh and dry weight of wild carrots was reported at the 12-week juvenile stage as 25.75 ± 2.13 g and 5.22 ± 0.45 g, respectively. These values were 33 % and 43 % greater than the comparable shoot fresh and dry weights of cultivated carrots. Furthermore, the shoot fresh and dry weights of wild and cultivated carrots were not significantly different ($p > 0.05$) at the 4-week juvenile stage. This illustrates a similar growth pattern of wild and cultivated carrots up to the first 4 weeks. Consequently, the growth trend of wild carrots is quicker than that of cultivated carrots in terms of the fresh and dry weight of the shoots (**Table 5.3**). Likewise, Grebenstein et al. (2013) found that wild carrots had greater shoot

dry weights than most carrot cultivars. The shoot features of wild and cultivated carrots differ mostly due to the genetic control of morphological traits (Grebenstein et al., 2013). Furthermore, between the 8 and 12 weeks of the juvenile phase, there was a dramatic rise in the shoot's fresh weight (by 80.5 %) and dry weight (by 82.57 %), which emphasizes a focus on managing wild carrots promptly (**Table 5.3**). Due to the variability in biomass at different growth stages, Stachler & Kells (1997) have recommended different combinations of herbicides to control wild carrots according to their growth stage (seedling, established and over-wintered wild carrots).

5.3.1.4. Root length and diameter

Investigating the growth pattern of root length and diameter is essential since the taproot is the economically valuable component of the cultivated carrot (Que et al., 2019). Due to this, root characteristics have been identified and become important criteria in breeding programmes (Macko-Podgórní et al., 2020). Furthermore, it is important to understand the wild carrot's growth pattern of below-ground parts from the perspective of weed management (Stachler et al., 2000). A significant variation ($p < 0.05$) was reported in root length and root diameter among wild and cultivated carrots at all the juvenile phases. The longest root was observed in wild carrots (19.79 ± 1.45 cm) at week 12 of the juvenile stage, which was 47.5 % higher than the root length of cultivated carrots. Whereas, cultivated carrots were shown to have a larger root diameter (23.78 ± 0.85 cm) in the 12 weeks of the juvenile phase, which was 58.8 % wider than wild carrots (**Table 5.3**). Genetic mechanisms are the key reasons for variations between wild and cultivated carrots regarding the shape and size of the roots (Grebenstein et al., 2013). Particularly, QTLs (quantitative trait locus) on chromosomes 1, 2, and 7 were concerned with regulating root length, while a 180 kb region on chromosome 1 was linked to root shoulder diameter (Macko-Podgórní et al., 2020; Chenggang Ou et al., 2022). Furthermore, a rapid increase in root length was found between the juvenile stages of 4 and 8 weeks, and the 8 and

12 weeks for cultivated and wild carrots, respectively (**Table 5.3**). Tilling the surroundings of the carrot seed-producing field can be an effective mechanical weed management method to control wild carrots from a long-term point of view (Stachler & Kells, 1997). Furthermore, wild carrot's deep taproot facilitates stock energy for the consequent regrowth and creates difficulties for removal (Praciak, 2015). Although some tillage tools, including rotary hoe, can till up to the depth of 15 cm, wild carrot produces taproots deeper than 19 cm after 12 weeks of the juvenile phase. Rome & Lucero (2019) noted that the partial removal of wild carrots' roots resulted in regeneration and the development of new sprouts in the subsequent seasons. Therefore, it is important to take root length into account and initiate tillage operations or hand-pulling methods to remove the entire plants as early as possible in the wild carrot's life cycle (Chauhan & Johnson, 2010).

5.3.1.5. Root fresh and dry weight

Root biomass is an economically important trait in cultivated carrots. However, this trait can vary between the genotypes of cultivated carrots (Singh et al., 2022). There was a significant difference ($p < 0.05$) between wild and cultivated carrots in terms of root fresh and dry weight. Moreover, the highest fresh and dry weight of cultivated carrots was recorded as 18.88 ± 1.51 g and 2.88 ± 0.33 g, respectively at the 12-week juvenile stage. Comparatively, cultivated carrots developed roots that were around three times as large as those of wild carrots (**Table 5.3**). A significant signature of cultivated carrots is the development of larger storage roots than wild species (Ou et al., 2022). Furthermore, the root fresh and dry weight of both cultivated and wild carrots increased with the increasing juvenile period. This increment was most rapid from 8 to 12 weeks of the juvenile stage for both wild and cultivated carrots compared with the early growth stages (**Table 5.3**). Schittenhelm & Schroetter (2014) have observed the adaptation of wild carrots to prolonged drought conditions via redistribution of root mass to

deeper soil layers. It is very challenging to manage wild carrots after they have increased most root biomass. Therefore, it is important to control wild carrots at the early juvenile stages.

Table 5.2 Analysis of variance (ANOVA) for morphological traits of wild and cultivated carrots (genotype) at different juvenile stages

Source of variation (S.O.V)	df	Mean square							
		Plant height	Number of leaves	Shoot fresh weight	Shoot dry weight	Root length	Root diameter	Root fresh weight	Root dry weight
Block	3	61 ^{ns}	76 [*]	199 ^{**}	8.79 ^{**}	87.3 ^{**}	4 ^{ns}	5 ^{ns}	3.35 ^{**}
Factor a (Genotype)	1	11 ^{ns}	2670 ^{**}	595 ^{**}	38.54 ^{**}	719.3 ^{**}	1383 ^{**}	748 ^{**}	5.43 ^{**}
Factor b (Juvenile period)	2	13287 ^{**}	3601 ^{**}	8479 ^{**}	315.26 ^{**}	2579.4 ^{**}	4108 ^{**}	3177 ^{**}	104.59 ^{**}
Factor a × b	2	23 ^{ns}	1159 ^{**}	352 ^{**}	23.49 ^{**}	390.4 ^{**}	883 ^{**}	727 ^{**}	7.29 ^{**}
Error	189	24	23	33	1.45	19.8	7	14	0.73

Note: df: Degrees of freedom; *, **: significantly different at the 5 % and 1 % probability level, respectively; ns: non-significant

Table 5.3 Effect (mean analysis) of different juvenile stages on morphological parameters of two different genotypes of carrots

Genotype	Juvenile period	Plant height (cm)	Number of leaves	Shoot fresh weight (g)	Shoot dry weight (g)	Root length (cm)	Root diameter (mm)	Root fresh weight (g)	Root dry weight(g)
Cultivated	12 weeks	38.05 ^a ±0.88	8.23 ^{bc} ±0.17	17.16 ^b ±1.01	2.98 ^b ±0.24	10.39 ^b ±0.65	23.78 ^a ±0.85	18.88 ^a ±1.51	2.88 ^a ±0.33
	8 weeks	25.52 ^a ±1.02	5.73 ^{cd} ±0.18	3.69 ^{cd} ±0.37	0.59 ^{cd} ±0.06	8.14 ^b ±0.57	7.68 ^c ±0.59	1.40 ^c ±0.25	0.16 ^c ±0.03
	4 weeks	8.92 ^a ±0.37	1.94 ^c ±0.08	0.09 ^d ±0.01	0.02 ^d ±0.003	2.65 ^c ±0.13	0.78 ^e ±0.06	0.01 ^c ±0.003	0.001 ^c ±1.69 × 10 ⁻⁴
Wild	12 weeks	35.95 ^a ±1.22	25.00 ^a ±1.81	25.75 ^a ±2.13	5.22 ^a ±0.45	19.79 ^a ±1.45	9.81 ^b ±0.53	6.98 ^b ±0.68	1.74 ^b ±0.21
	8 weeks	25.84 ^a ±0.94	10.34 ^b ±0.80	4.93 ^c ±0.79	0.91 ^c ±0.13	9.89 ^b ±0.84	4.91 ^d ±0.30	0.75 ^c ±0.13	0.17 ^c ±0.02
	4 weeks	8.35 ^a ±0.35	2.50 ^{de} ±0.10	0.08 ^d ±0.01	0.02 ^d ±0.003	2.80 ^c ±0.24	0.75 ^e ±0.04	0.01 ^c ±0.003	0.002 ^c ±2.24 × 10 ⁻⁴

Note: Means followed by the same letter(s) in each column are not significantly different based on Tukey's Test

5.3.2. Correlation analysis

Estimation of the relationship between the morphological traits of wild carrots and commercial carrots via correlation studies can provide details that will help scientists and agronomists in determining the most efficient weed management strategies to control wild carrots in carrot seed-producing regions globally (Simon et al., 2021; Turner et al., 2018). The strength of the correlation coefficients among the examined morphological characteristics also demonstrated how important it is to comprehend how they relate to one another in order to implement sustainable weed management practices (Mennan et al., 2020). Especially, this evaluation is important to understand the relationship between the above (plant height, leaf number, and shoot fresh and dry weight) and below-ground (root length, root diameter, and root fresh and dry weight) morphological traits of both wild and cultivated carrots, which will help in decision making based on the morphological development of above-ground parts without needing to uproot the plants. The results obtained from the correlation analysis of the morphological traits of wild and cultivated carrots are shown in **Figure 5.2**. Pearson's correlation coefficient (r) revealed a significant ($p < 0.05$) relationship among all the morphological traits of wild and cultivated carrots. The plant height of cultivated carrots was positively and strongly correlated with root length ($r = 0.783$), root diameter ($r = 0.897$), and root fresh weight ($r = 0.728$). It also showed that the leaf number of cultivated carrots positively and strongly correlated with root length ($r = 0.764$), root diameter ($r = 0.887$), and root fresh weight ($r = 0.740$). Furthermore, the root diameter ($r = 0.958$) and root fresh weight ($r = 0.894$) of cultivated carrots showed a positive correlation with shoot fresh weight. Moreover, there was a strong and positive correlation ($r = 0.908$) between the root diameter and root fresh weight of cultivated carrots. Pearson correlation matrix between the morphological traits of wild carrots indicated that root fresh weight was positively correlated with plant height, number of leaves, shoot fresh weight, root length, and root diameter. This positive correlation was strong with shoot fresh weight (r

= 0.848) and root diameter ($r = 0.839$); and moderate with plant height ($r = 0.647$), number of leaves ($r = 0.695$), and root length ($r = 0.675$). Furthermore, root diameter ($r = 0.863$) and length ($r = 0.732$) had a positive and strong correlation with plant height in wild carrot plants. Also, both root length and diameter were positively correlated with the number of leaves ($r = 0.660$ and $r = 0.796$, respectively) and shoot fresh weight ($r = 0.662$ and 0.879 , respectively). Similar positive correlations have been reported by Singh et al. (2021) and Fanlégué et al. (2017) in Indian carrot genotypes and hybrid carrot varieties in Ivory Coast, respectively. The positive correlation between the root diameter, root length and root fresh weight with plant height, number of leaves and shoot fresh weight may be accounted for by the higher photosynthetic rates (Islam et al., 1998). These findings indicated that the plant height, number of leaves and shoot fresh weight can be used as root trait predictors of both wild and cultivated carrots.

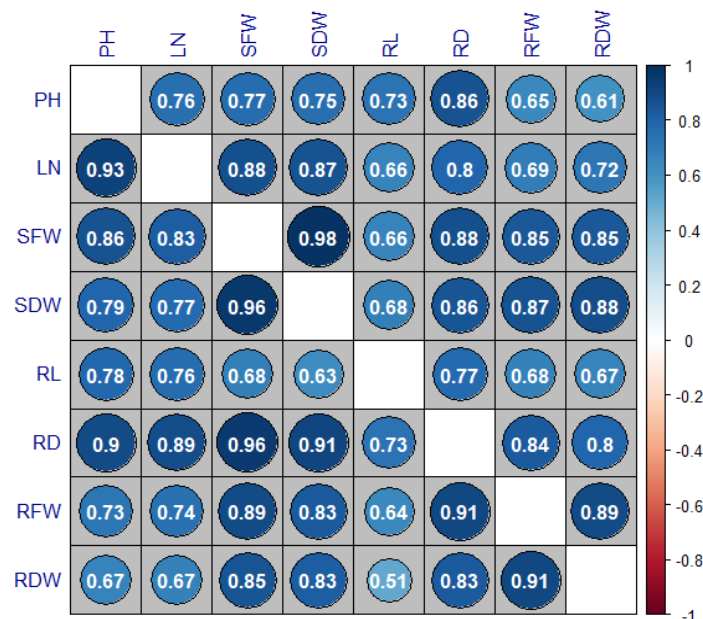


Figure 5.2 Correlation matrix between morphological traits of wild and cultivated carrots; Upper diagonal-wild carrots and lower diagonal-cultivated carrots; keys: PH- plant height, LN- Leaves number, SFW- shoot fresh weight, SDW- shoot dry weight, RL-root length, RD-root diameter, RFW- root fresh weight, RDW- root dry weight.

5.3.3. Principal component analysis

Principal component analysis (PCA) is an analysis method that is frequently used to assist in data exploration and visualization by highlighting variance and revealing significant trends in the dataset (Ashrafi et al., 2023). In this study, PCA was done to understand the relative contribution of different morphological traits for evaluating the phenological variability among the wild and cultivated carrots. To facilitate graphical displays of such data matrices, biplot axes were created after estimating eigenvalues, which serve as essential in numerical diagnostics to assess the variation among the 8 morphological variables of both wild and cultivated carrots (Gyawali et al., 2021). Accordingly, the entire variation was split up into 8 principal components (PCs) and a scree plot was generated to display the percentage of variance. The PCA produced two PC groups with an eigenvalue of more than 1, accounting for 86.5 % variability (PC 1, 69.6 % and PC 2, 16.9 %) (**Figure 5.3**). Furthermore, it is evident that all morphological characteristics contribute more to PC 1 than PC 2 based on the correlation between morphological traits and PCs (**Table 5.4**). Therefore, cultivated carrots can be distinguished from wild carrots by using morphological traits such as plant height, leaf number, shoot dry and fresh weights, root diameter, root length, and root dry and fresh weight. Consequently, all the morphological traits of wild and cultivated carrots were plotted against PC 1 and PC 2 (**Figure 5.4**).

The findings from PCA indicated that the wild and cultivated carrots could be effectively distinguished and categorized by PC 1 and PC 2 since the PCA biplots clearly clustered the wild and cultivated carrots based on the morphological traits at the vegetative stages (**Figure 5.4**). Furthermore, we found two sets of morphological traits that could differentiate the wild and cultivated carrots from each other in different directions on the PCA biplot (PC 1 vs PC 2). The first group of root-related morphological traits, including RD (root diameter), RFW (root fresh weight), and RDW (root dry weight), showed a positive correlation with one another and

the second set of traits included RL (root length), LN (leaves number), SFW (shoot fresh weight), and SDW (shoot dry weight), which efficiently separated among the wild and cultivated carrots in two different quadrants. Moreover, the genotype cluster of cultivated and wild carrots was inclined toward the first and second set of morphological traits, respectively. These findings indicated that wild and cultivated carrots exhibited a significant degree of variability in terms of morphological traits except PH (plant height). The representation from PC 1 and PC 2 illustrates considerable amounts of overlap from left to right (PC 1) and top to bottom (PC2), which is mainly due to the presence of similar morphological characteristics of both wild and cultivated carrots at their early vegetative stage (prior to 4 weeks of age).

Table 5.4 Correlation of all morphological traits to PC 1 and PC 2 for wild and cultivated carrots.

Morphological trait	PC 1	PC 2
PH	0.872	-0.002
LN	0.735	0.602
RL	0.742	0.389
RD	0.816	-0.507
SFW	0.938	0.212
RFW	0.789	-0.566
SDW	0.913	0.272
RDW	0.848	-0.372

Note: PH- plant height, LN- Leaves number, SFW- shoot fresh weight, SDW- shoot dry weight, RL- root length, RD- root diameter, RFW- root fresh weight, RDW- root dry weight

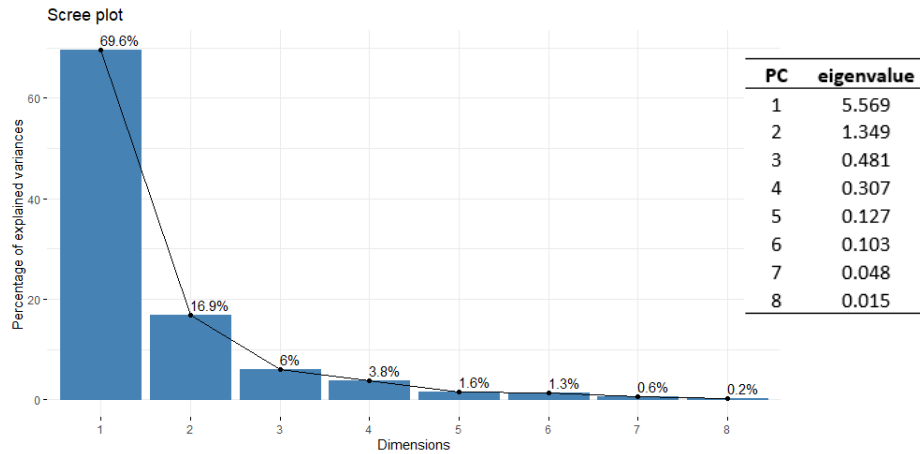


Figure 5.3 Scree plot of variability % against the number of PCs for morphological attributes and a table for PCs Vs eigenvalue

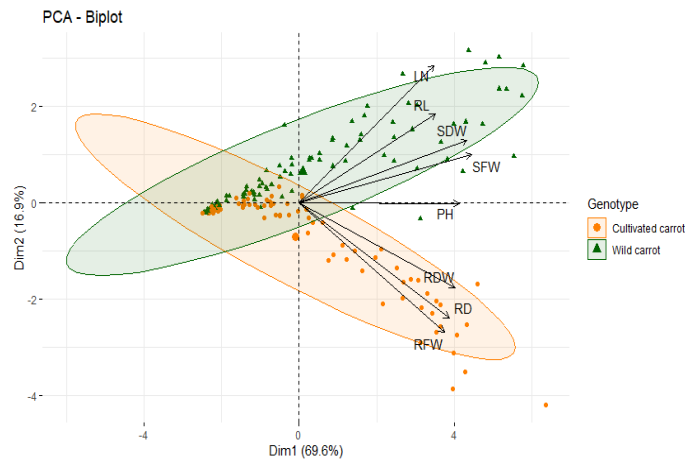


Figure 5.4 Principal component analysis of wild and cultivated carrots based on the morphological parameters. These parameters included PH (Plant height), LN (Leaves number), SFW (Shoot fresh weight), SDW (Shoot dry weight), RL (Root length), RD (Root diameter), RFW (Root fresh weight), and RDW (Root dry weight). The scatter plot displays the distribution of sampled plants (either wild or cultivated) according to PC 1 and PC 2.

5.3.4. Modelling the growth pattern of wild and cultivated carrots

5.3.4.1. Model estimation

The summary statistics for the predicted models of cultivated and wild carrots are shown in **Table 5.5** and **Table 5.6**, respectively. The growth patterns of both cultivated and wild carrots throughout the juvenile phase were modelled using the linear, quadratic, exponential and power functions (Paine et al., 2012). The mathematical functions chosen to simulate and predict the growth of wild and cultivated carrot plants have been selected based on the statistical criteria. Preferred models attain higher R^2 and $adj-R^2$, but lower $RMSE$, AIC and BIC (León-Burgos et al., 2022). The key reason for using four different statistical criteria is to obtain more accurate models by eliminating model overfitting issues (Xing et al., 2013).

The plant height ($R^2 = 0.857$; $RMSE = 0.245$), leaf number ($R^2 = 0.894$; $RMSE = 0.214$), shoot fresh weight ($R^2 = 0.910$; $RMSE = 0.706$), root diameter ($R^2 = 0.920$; $RMSE = 0.422$), root fresh weight ($R^2 = 0.913$; $RMSE = 1.128$), and root dry weight ($R^2 = 0.906$; $RMSE = 1.034$) of cultivated carrots were fitted to power regression growth pattern, whereas a quadratic function was used to model the shoot dry weight ($R^2 = 0.867$; $RMSE = 0.441$). Instead, for wild carrots, power regression models were used to fit the growth curves resulting from plant height ($R^2 = 0.847$; $RMSE = 0.255$), leaf number ($R^2 = 0.837$; $RMSE = 0.387$), shoot fresh weight ($R^2 = 0.892$; $RMSE = 0.816$), shoot dry weight ($R^2 = 0.896$; $RMSE = 0.746$), root diameter ($R^2 = 0.861$; $RMSE = 0.414$), root fresh weight ($R^2 = 0.888$; $RMSE = 1.059$) and root dry weight ($R^2 = 0.880$; $RMSE = 0.993$). Low R^2 values can signal that a forecast is not precise (Sharifi, 2020). Hence, the root length of the cultivated carrot was removed from the model prediction due to the comparatively low regression coefficient ($R^2 < 0.75$). Furthermore, Vega Rojas et al. (2012) showed exponential patterns in the growth of five different hybrid carrot varieties in the Costa Rica region during the early vegetative phase (from 0 to 100 days). This demonstrates the regional variance in the growth pattern of carrot genotypes in their vegetative phase.

5.3.4.2. Model validation

Model validation is typically used to verify that the chosen models are adequate representations of the real system and to confirm the model's representation of the experimental values is accurate (Basak et al., 2019). A validation set of 30 % of the total data, that was not included in the model estimation, was examined in order to validate four different regression models (linear, quadratic, exponential, and power) (Nguyen et al., 2021). The relationship between the predicted and actual values from the validation data set for selected morphological traits of cultivated and wild carrots is illustrated in **Figure 5.5** and **Figure 5.6**, respectively. Model validation results indicated that the power regression model was the best to predict the growth pattern of plant height ($R^2 = 0.879$), leaf number ($R^2 = 0.9159$), shoot fresh weight ($R^2 = 0.8068$), root diameter ($R^2 = 0.8475$), and root fresh weight ($R^2 = 0.7782$) of cultivated carrots. However, due to the lower R^2 value, models related to the root dry weight ($R^2 = 0.6888$) and shoot dry weight ($R^2 = 0.6748$) of cultivated carrots were excluded from the model prediction. Similarly, the power regression model was shown to be the most accurate in predicting the growth patterns of wild carrots regarding plant height ($R^2 = 0.8807$), leaf number ($R^2 = 0.8508$), shoot fresh weight ($R^2 = 0.8443$), shoot dry weight ($R^2 = 0.827$), root diameter ($R^2 = 0.8209$), and root fresh weight ($R^2 = 0.7587$). On the other hand, root length ($R^2 = 0.697$) and root dry weight ($R^2 = 0.5442$) of wild carrots were not considered for the model prediction due to their inaccuracy.

The findings of the fitted growth curves provided in this study may be utilized to support recommendations for weed control methods during the early growth stage of wild carrots. In particular, the fitted equations can be applied to forecast the wild carrots' growth stage. The wild carrots might then be controlled using the appropriate weed control techniques, such as hand weeding, hoeing, mowing, tilling, and herbicide application according to their growth stages.

Table 5.5 Fitted models to estimate predicted values of different morphological traits of cultivated carrots as a function of duration from sowing (time)

	R²	Adj. R²	RMSE	AIC	BIC	Derived equation
<i>Plant height (PH)</i>						
Linear	0.868	0.866	4.450	396.197	402.811	PH _{CL} = 3.492T - 4.464
Quadratic	0.870	0.866	4.419	397.241	406.059	PH _{CQ} = -0.071T ² + 4.615T - 8.173
Log-linear	0.823	0.821	0.272	21.901	28.515	PH _{CE} = 4.6715e ^{0.1796T}
Log-log	0.857	0.855	0.245	7.728	14.342	PH _{CP} = 1.4573T ^{1.3121}
<i>No of leaves (LN)</i>						
Linear	0.884	0.882	0.913	183.968	190.582	LN _{CL} = 0.771T - 0.923
Quadratic	0.903	0.900	0.834	173.882	182.700	LN _{CQ} = -0.049T ² + 1.557T - 3.521
Log-linear	0.838	0.835	0.265	18.259	24.873	LN _{CE} = 1.0045e ^{0.1841T}
Log-log	0.894	0.893	0.214	-10.330	-3.716	LN _{CP} = 0.2944T ^{1.3622}
<i>Shoot fresh weight (SFW)</i>						
Linear	0.777	0.774	3.417	360.792	367.406	SFW _{CL} = 1.95T - 9.144

Quadratic	0.869	0.865	2.616	327.001	335.820	$SFW_{CQ} = 0.293T^2 - 2.709T + 6.246$
Log-linear	0.880	0.878	0.813	168.380	174.994	$SFW_{CE} = 0.0065e^{0.6729T}$
Log-log	0.910	0.908	0.706	149.540	156.154	$SFW_{CP} = 9E-05T^{4.8981}$
<i>Shoot dry weight (SDW)</i>						
Linear	0.773	0.770	0.575	122.052	128.666	$SDW_{CL} = 0.325T - 1.524$
Quadratic	0.867	0.863	0.441	88.338	97.157	$SDW_{CQ} = 0.049T^2 - 0.459T + 1.065$
Log-linear	0.901	0.900	0.705	149.336	155.950	$SDW_{CE} = 0.0014e^{0.6501T}$
Log-log	0.928	0.927	0.600	127.709	134.323	$SDW_{CP} = 2E-05T^{4.7252}$
<i>Root length (RL)</i>						
Linear	0.548	0.541	2.989	342.870	349.484	$RL_{CL} = 1.005T - 1.108$
Quadratic	0.558	0.545	2.954	343.288	352.107	$RL_{CQ} = -0.061T^2 + 1.973x - 4.305$
Log-linear	0.551	0.544	0.492	101.174	107.788	$RL_{CE} = 1.4316e^{0.1667T}$
Log-log	0.589	0.583	0.471	95.286	101.900	$RL_{CP} = 0.4705T^{1.234}$
<i>Root diameter (RD)</i>						
Linear	0.856	0.854	3.793	374.766	381.381	$RD_{CL} = 2.825T - 12.099$
Quadratic	0.917	0.914	2.886	340.181	349.000	$RD_{CQ} = 0.328T^2 - 2.389T + 5.124$

Log-linear	0.905	0.904	0.459	91.673	98.287	$RD_{CE} = 0.148e^{0.4329T}$
Log-log	0.920	0.919	0.422	80.386	87.000	$RD_{CP} = 0.0096T^{3.1248}$
<i>Root fresh weight (RFW)</i>						
Linear	0.609	0.603	5.839	432.585	439.199	$RFW_{CL} = 2.228T - 11.348$
Quadratic	0.768	0.761	4.496	399.575	408.394	$RFW_{CQ} = 0.496T^2 - 5.666T + 14.73$
Log-linear	0.902	0.901	1.195	220.057	226.671	$RFW_{CE} = 4E-05e^{1.1103T}$
Log-log	0.913	0.912	1.128	212.318	218.932	$RFW_{CP} = 3E-08T^{7.9972}$
<i>Root dry weight (RDW)</i>						
Linear	0.490	0.482	1.032	200.339	206.953	$RDW_{CL} = 0.309T - 1.582$
Quadratic	0.625	0.613	0.885	181.748	190.567	$RDW_{CQ} = 0.071T^2 - 0.816T + 2.134$
Log-linear	0.904	0.902	1.046	196.330	202.853	$RDW_{CE} = 2E-05e^{0.98662T}$
Log-log	0.906	0.905	1.034	194.842	201.365	$RDW_{CP} = 4E-08T^{7.0968}$

Note: T, time from sowing (weeks); c; cultivated carrot; L- linear; Q- quadratic; E- exponential; P- power;

R^2 , coefficient of determinant; *adj. R²*, adjusted coefficient of determinant, *RMSE*, root mean square

error; *AIC*, Akaike Information Criteria; *BIC*, Bayesian information criterion

Table 5.6 Fitted models to estimate predicted values of different morphological traits of wild carrots as a function of duration from sowing (time)

	R ²	Adj. R ²	RMSE	AIC	BIC	Derived equation
<i>Plant height (PH)</i>						
Linear	0.761	0.757	6.153	471.969	478.799	PH _{WL} = 3.417T - 3.857
Quadratic	0.783	0.776	5.864	467.030	476.137	PH _{WQ} = -0.246T ² + 7.402T - 17.454
Log-linear	0.782	0.779	0.303	38.551	45.381	PH _{WE} = 4.6202e ^{0.1793T}
Log-log	0.847	0.844	0.255	13.439	20.269	PH _{WP} = 1.2981T ^{1.3604}
<i>No of leaves (LN)</i>						
Linear	0.582	0.577	7.544	501.306	508.136	LN _{WL} = 2.777T - 9.795
Quadratic	0.598	0.586	7.403	500.596	509.703	LN _{WQ} = 0.191T ² - 0.320T + 0.774
Log-linear	0.823	0.821	0.403	79.334	86.164	LN _{WE} = 0.9282e ^{0.2706T}
Log-log	0.837	0.835	0.387	73.472	80.302	LN _{WP} = 0.1552T ^{1.9906}
<i>Shoot fresh weight (SFW)</i>						

Linear	0.567	0.561	8.968	526.211	533.041	$SFW_{WL} = 3.2T - 15.602$
Quadratic	0.629	0.618	8.309	517.216	526.322	$SFW_{WQ} = 0.445T^2 - 4.01T + 9.002$
Log-linear	0.852	0.850	0.956	203.786	210.616	$SFW_{WE} = 0.0056e^{0.7155T}$
Log-log	0.892	0.891	0.816	180.992	187.822	$SFW_{WP} = 4E-05T^{5.3403}$
<i>Shoot dry weight (SDW)</i>						
Linear	0.560	0.553	1.883	301.434	308.264	$SDW_{WL} = 0.661T - 3.274$
Quadratic	0.632	0.621	1.721	290.521	299.628	$SDW_{WQ} = 0.101T^2 - 0.968T + 2.287$
Log-linear	0.864	0.863	0.851	187.082	193.912	$SDW_{WE} = 0.0018e^{0.6698T}$
Log-log	0.896	0.894	0.746	168.156	174.986	$SDW_{WP} = 2E-05T^{4.973}$
<i>Root length (RL)</i>						
Linear	0.563	0.557	5.706	461.113	467.943	$RL_{WL} = 2.018T - 5.633$
Quadratic	0.567	0.554	5.682	462.495	471.602	$RL_{WQ} = 0.07T^2 + 0.891T - 1.788$
Log-linear	0.683	0.678	0.519	115.922	122.752	$RL_{WE} = 1.0839e^{0.2374T}$
Log-log	0.705	0.701	0.501	110.723	117.553	$RL_{WP} = 0.2197T^{1.7598}$
<i>Root diameter (RD)</i>						
Linear	0.733	0.729	2.179	322.482	329.312	$RD_{WL} = 1.125T - 3.846$

Quadratic	0.734	0.726	2.175	324.220	333.327	$RD_{wQ} = 0.017T^2 + 0.845T - 2.889$
Log-linear	0.808	0.806	0.485	106.210	113.040	$RD_{wE} = 0.2625e^{0.3106T}$
Log-log	0.861	0.859	0.414	83.213	90.043	$RD_{wP} = 0.0302T^{2.3377}$
<i>Root fresh weight (RFW)</i>						
Linear	0.515	0.508	2.789	358.043	364.873	$RFW_{wL} = 0.8958T - 4.6546$
Quadratic	0.614	0.603	2.488	343.605	352.712	$RFW_{wQ} = 0.166T^2 - 1.796T + 4.533$
Log-linear	0.854	0.852	1.209	237.613	244.443	$RFW_{wE} = 0.0001e^{0.9098T}$
Log-log	0.888	0.886	1.059	218.556	225.386	$RFW_{wP} = 3E-07T^{6.7669}$
<i>Root dry weight (RDW)</i>						
Linear	0.452	0.444	0.800	178.127	184.957	$RDW_{wL} = 0.226T - 1.187$
Quadratic	0.546	0.533	0.727	166.471	175.577	$RDW_{wQ} = 0.044T^2 - 0.484T + 1.237$
Log-linear	0.854	0.852	1.097	220.608	227.396	$RDW_{wE} = 7.5E-05e^{0.8312T}$
Log-log	0.880	0.878	0.993	206.475	213.263	$RDW_{wP} = 3E-07T^{6.1706}$

Note: T, time from sowing (weeks); w; wild carrot; L- linear; Q- quadratic; E- exponential; P- power; R^2 , coefficient of determinant; *adj. R²*, adjusted coefficient of determinant, *RMSE*, root mean square error; *AIC*, Akaike Information Criteria; *BIC*, Bayesian information criterion

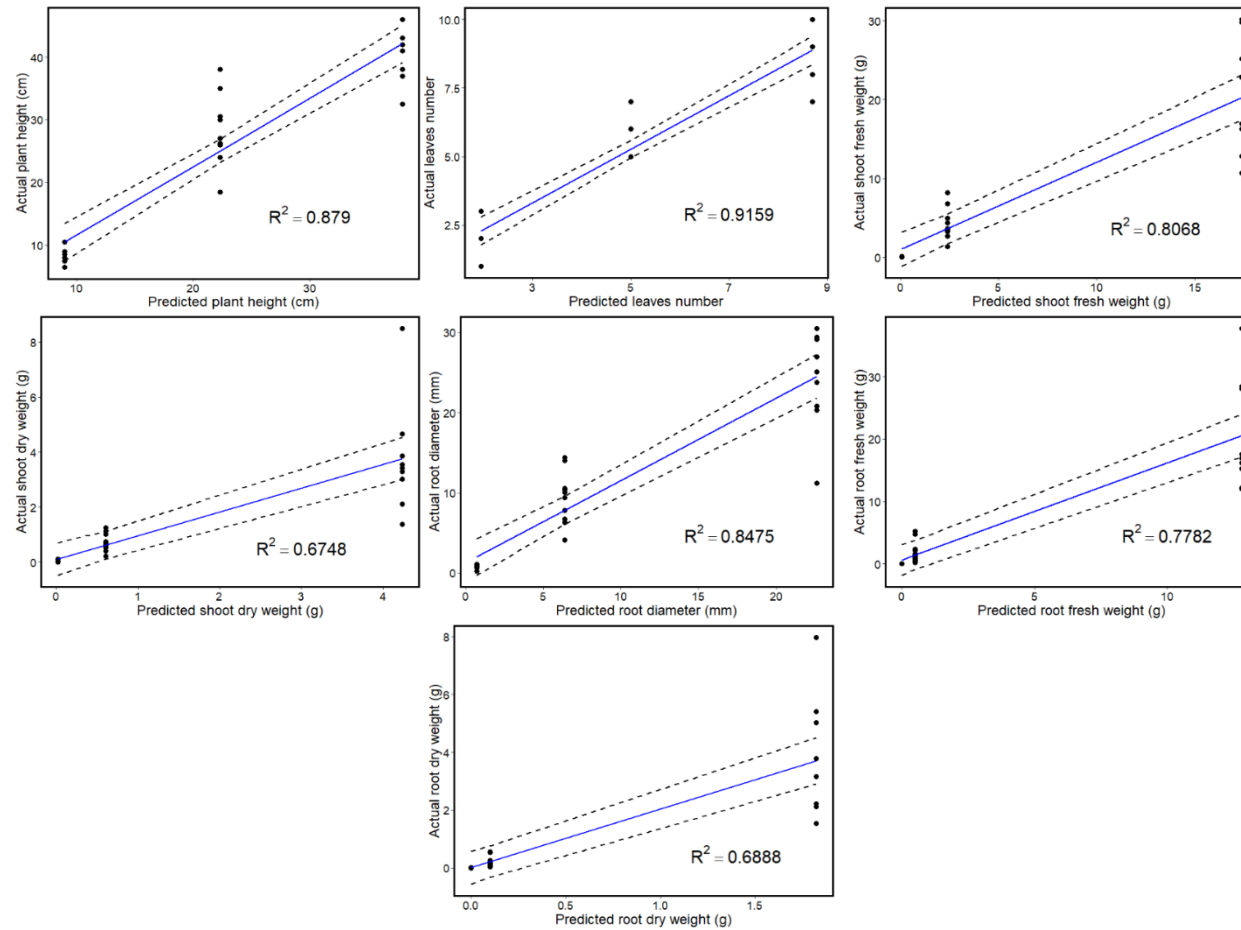


Figure 5.5 Predicted values vs actual values for validation data set using selected regression models of the morphological traits of cultivated carrots. The solid and dotted lines represent the predicted line and the confidence interval bounds, respectively.

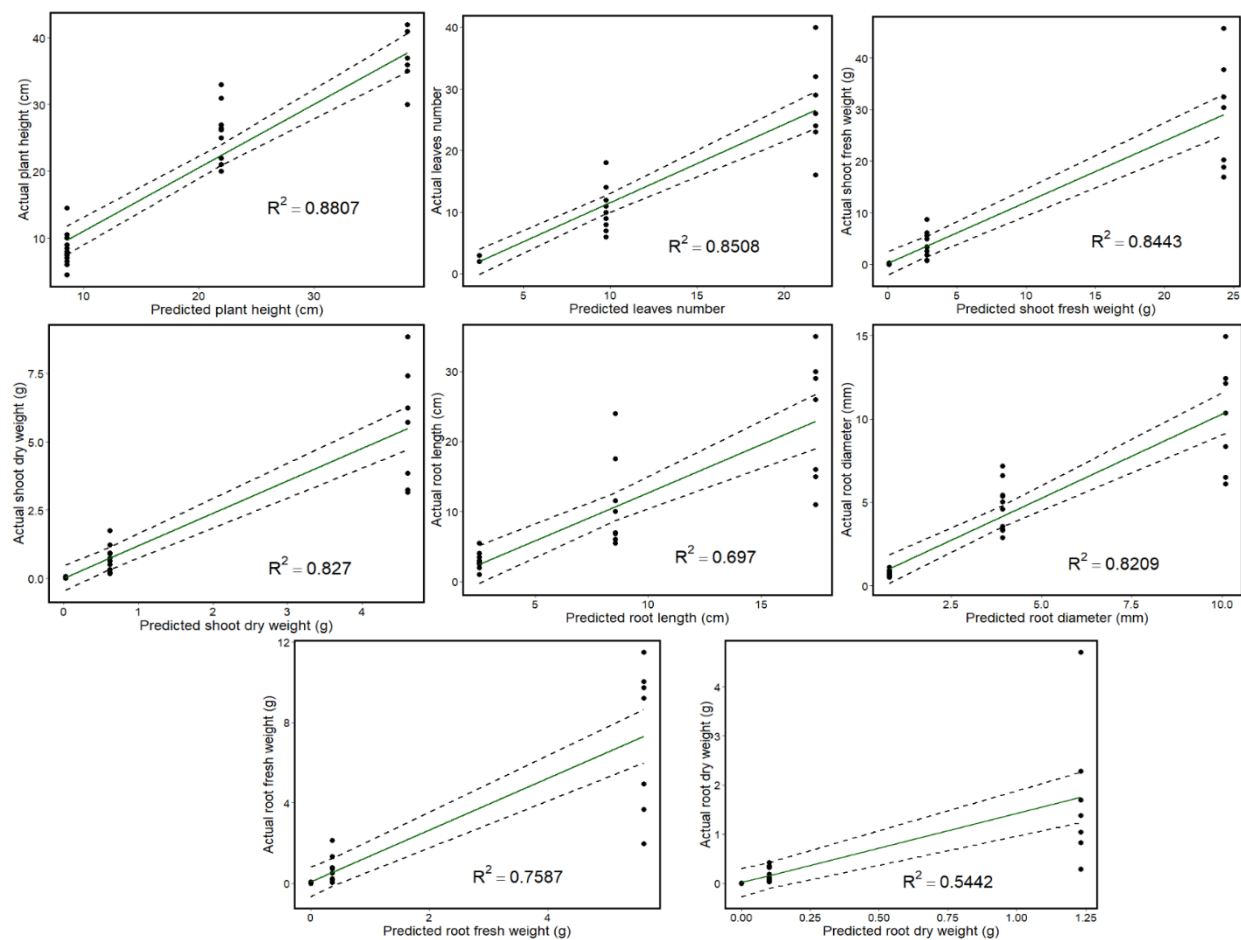


Figure 5.6 Predicted values vs actual values for validation data set using selected regression models of the morphological traits of wild carrots. The solid and dotted lines represent the predicted line and the confidence interval bounds, respectively.

5.4. Conclusion

The primary objective of this study was to assess and model the growth of different morphological traits in both wild and cultivated carrots during their juvenile phase using various statistical approaches. The effect of juvenile period and genotype on the vegetative growth of wild and cultivated carrots was studied using ANOVA statistical methods. Comparatively, wild carrots grew much faster than cultivated carrots in terms of leaf number, shoot fresh weight, shoot dry weight and root length. The growth of these traits was most rapid after 8 weeks of the juvenile stage (9-11 leaves stage). Therefore, it is important to manage the wild carrots before the 9-11 leaves stage. Furthermore, wild carrots can produce taproots of 200 mm in length at the end stage of the juvenile phase. To completely remove the taproot of the wild carrot from the soil profile (thus limiting the possibility of regrowth), the depth of the taproot should be considered whilst selecting tillage implements. Likewise, manual weeding should also be done before the stage of 9-11 leaves, at which point the entire wild carrot plant, including the taproot, can be easily pulled out. Meanwhile, when selecting a recommended herbicide to spray, it's crucial to have a better understanding of the wild carrot's growth pattern because the type of herbicide and the rate of application varies according to the stage of growth. Correlation analysis indicated a significant and strong positive correlation between most of the above and below-ground morphological traits of both wild and cultivated carrots. Therefore, decisions impacted by root length, diameter, and weight can be made without uprooting the plants using the above-ground traits, such as plant height and leaf count, because they are easier to measure. PCA results revealed that the wild and cultivated carrots can be distinguished based on morphological traits other than plant height. To model the growth pattern of eight different morphological traits of both wild and cultivated carrots, several regression models were analyzed and discussed in this work. In the field of agriculture, regression models are

also frequently used to forecast the complex growth pattern of plant morphological characteristics. Even though four different models were developed from the training data set (70 % of the sample), a power regression model was recommended based on the statistical criteria, such as R^2 , $adj-R^2$, $RMSE$, AIC and BIC to predict all the morphological traits of wild and cultivated carrots except shoot dry weight and root length of cultivated carrots due to the lower accuracy of the model. Instead, a quadratic model was suggested to estimate the growth pattern of the shoot dry weight of cultivated carrots. Validation of the recommended models, especially the quadratic and power model, using the validation data set (30 % of the sample) revealed a positive relationship ($R^2 > 0.75$) between the predicted and actual data of the selected morphological traits of wild and cultivated carrots from the training data set, except the cultivated carrot's shoot and root dry weights and root length and dry weight of wild carrots. The results of the modelling study indicated that the power regression model can be used to predict the growth pattern of plant height, number of leaves, shoot fresh weight, shoot dry weight (only for wild carrots), root diameter, and root fresh weight of both wild and cultivated carrots. The incorporation of data regarding morphological traits with a growth model provides an efficient tool to enhance the wild carrot management, as plant height, a readily measurable trait can be used to determine the growth stage in the absence of known seeding time. This enables non-destructive prediction of other traits (e.g., root length, leaf number), facilitating timely and effective management decisions. Moreover, studying the growth pattern of cultivated carrot's morphological traits is beneficial for the farmers, who produce taproots for consumption and steckling production. Furthermore, the findings of this study suggest the significance of incorporating the growth pattern of wild carrots in formulating weed management strategies to prevent their spread. This study also provides information for the decision-making at the farm level and development of regionally specific weed management

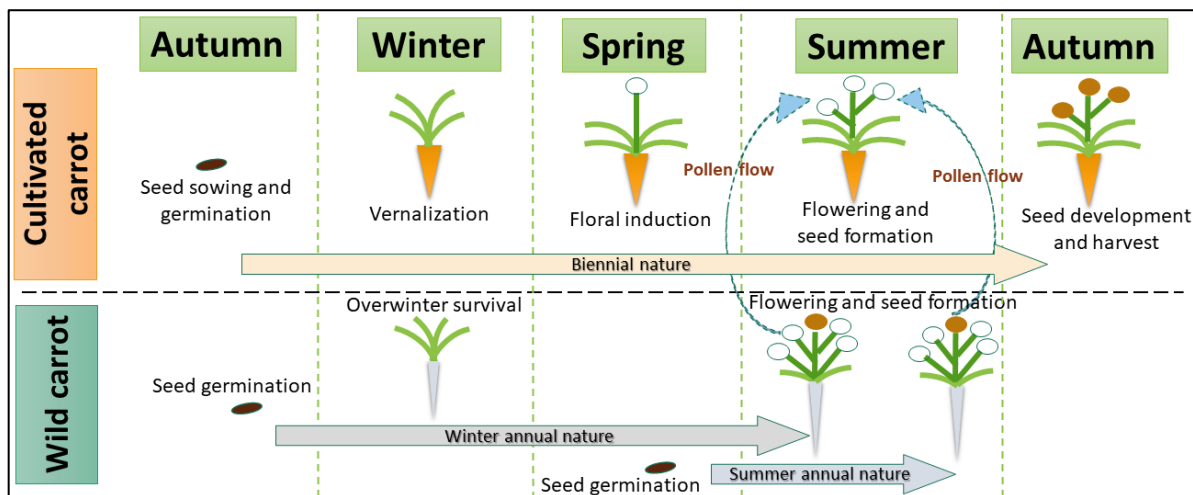
practices, suppression of wild carrot infestation, and prevention of seed production. In conclusion, these findings considerably advance our current knowledge of managing wild carrots, particularly in the areas around commercial carrot seed production sites. As a last point, we would like to emphasize that this study appears to be the first in the literature to compare and model the vegetative growth pattern of wild and cultivated carrot genotype (No 27 Male lines) in New Zealand.

Chapter 6: Effects of different juvenile periods and vernalization requirements on flowering behaviour of wild and cultivated carrots

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The results presented in Chapter 5 demonstrated that the wild carrots must be controlled before the 9–11 leaves stage due to their rapid growth habit in the later part of the vegetative phase compared to cultivated carrots. The next vital step is to study the reproductive phase of wild and cultivated carrots, focusing on their requirement for juvenility and vernalization. Thus, a pot experiment presented in Chapter 6 studied the interaction effects of juvenility and vernalization on flowering and floral characteristics of both wild and cultivated carrots, as well as the life cycle and floral morphology of wild carrots in New Zealand.

Graphical abstract



Abstract

Comparing the life cycles strategies (annual and biennial) of wild and cultivated carrots, particularly in relation to juvenility and vernalization requirements, is vital for identifying any overlapping flowering periods, as wild carrots have the potential to compromise the genetic purity of commercial carrot seeds via pollen flow. However, little information is known about how juvenility, vernalization, and their interactions impact the flowering pattern of wild and cultivated carrots in New Zealand. Therefore, a pot experiment was conducted to evaluate the influence of different juvenile phases (J_1 -12 weeks, J_2 - 8 weeks, and J_3 - 4 weeks), and vernalization phases (V_1 - 12 weeks, V_2 - 4 weeks, and V_3 - no vernalization) on floral characteristics and flowering behaviour of cultivated (G_1) and wild (G_2) carrots. The study was executed in a factorial ($2 \times 3 \times 3$) randomized complete block design with 4 blocks of 5 plants per block. Observations on flowering percentage, time taken for flowering, percentage of over-winter survival, number of umbels and branches, and height of floral stem were recorded and analyzed as a 3-way ANOVA. Flowering of cultivated carrots was observed only when they were exposed to a 12-week vernalization treatment. Wild carrots showed 100 % flowering across all treatment combinations. Wild carrots exhibited a higher overwintering survival rate (94.9% - 100%) compared with cultivated carrots (66.1% - 98.3%). The study demonstrates that the cultivated carrot is grown as a biennial, whereas wild carrots can establish themselves as either summer annual or winter annual in New Zealand. It is recommended to utilise the different life cycles of wild and cultivated carrots to minimize the pollen flow from wild to cultivated carrots via implementing timely weed management strategies.

Keywords: *Daucus* species, floral induction, life cycle, New Zealand, temperature, Umbels

6.1 Introduction

Invasive weed species are alien plants that pose serious threats to natural ecosystems and result in substantial economic losses in agriculture (Wang et al., 2024). Due to their unique evolutionary mechanisms, invasive weeds have shown rapid adaptation to various climate change scenarios, often outperforming native species (Sun et al., 2023). Factors such as altered moisture regimes, rising atmospheric temperatures, and extreme climate events affect all plants, but invasive weeds can manipulate their life cycles and migrate to new regions more efficiently (Rathee et al., 2023). Consequently, weed infestations are considered as one of the major challenges to crop production (Datta et al., 2021; Ziska, 2022), sometimes leading to yield losses of up to 100 % in extreme cases (Damalas & Koutroubas, 2022).

Naturally, domesticated and cultivated crops have evolved from their weedy wild relatives (Kashyap et al., 2022). Hence, the invasion of wild populations adjacent to their domesticated close relatives has been a concern because of the gene flow between wild and cultivated species, which compromises the genetic purity of the seeds produced from cultivated commercial cultivars (Renzi et al., 2021). When both the spatial distribution and flowering are occurring simultaneously in the field, the instances of pollen flow between cultivated species and their wild relatives may be very high (Yook et al., 2021). This issue has been broadly observed throughout the world in commercial carrot seed production, where cultivated carrots (*Daucus carota* L. subsp. *sativus*) can readily hybridize with wild carrots (*Daucus carota* L. subsp. *carota*) since both are sexually compatible (Mandel & Brunet, 2019).

Wild carrot is considered an invasive weed, causing a significant threat to commercial carrot seed production (Hauser & Bjørn, 2001; Rome & Lucero, 2019). Wild carrots are particularly common along road edges, where they grow as a roadside plant. It is also found in waste areas, gardens,

cultivated lands, and ungrazed or unmown paddocks (Derrick, 2016; James et al., 2012). Under ideal environmental conditions, wild carrots can grow to a height of 1 m (Soltani et al., 2017). In addition, wild carrot produces a vast quantity of flowers, approximately 14,000 per plant in the field, which indicates the importance of controlling the wild carrots before flowering (Koul et al., 1989). *Daucus carota* species, including wild and cultivated carrots, have the ability to attract a wide variety of possible pollinators such as leaf cutting bees, honeybees, hoverflies, nectar scarabs, muscoid flies, European Blue Blow Flies, and various other wild bees (Davidson et al., 2010; Gaffney et al., 2018; Howlett, 2012; Howlett et al., 2015; Palmieri et al., 2019). Furthermore, higher outcrossing incidences (around 96 %) and long-lasting pollen viability (up to 10 days) of wild carrots result in a significant incidence of pollen flow to cultivated carrots (Rong et al., 2010; Umehara et al., 2005). Pollen transmission from wild to cultivated carrots can reduce the genetic purity of commercial carrot seeds due to undesirable outcrossing (Mandel & Brunet, 2019; Yahyaa et al., 2018). Therefore, it is important to understand the flowering pattern of wild and cultivated carrots to preserve quality carrot seed production.

The bolting and flowering of cultivated carrots are affected by several factors such as cardinal temperature, juvenility, and vernalization. These requirements, however, differ from cultivar to cultivar (Atherton et al., 1990). Carrot seedlings are receptive to vernalization signals only after a minimal period of development known as the juvenile phase (Villeneuve & Latour, 2017). When carrot plants have 8 to 12 leaves and storage roots that are greater than 4 to 8 mm in diameter, the juvenile period is considered completed (Atherton et al., 1990). Complex vernalization signalling networks have developed in carrots to detect variations in temperature (cold temperature: 5 °C) and photoperiod (short-day condition), which in turn regulates the time of flowering (Wohlfeiler et al., 2022). Moreover, the length of vernalization required is determined by the growth and size

of the plants attained during the juvenile phase, with more developed plants requiring a shorter period of vernalization (Samuolienė et al., 2008). During the transition from vegetative to reproductive phase via vernalization, the vegetative apical meristem converts into an elongated reproductive conical meristem, followed by the elongation of the inflorescence apex (Borthwick, 1931).

Carrots can be classified as annuals and biennials depending on the vernalization requirement, which is a genetically and geographically controllable trait. Generally, annuals require a shorter vernalization period (5-30 days) than biennials (11-12 weeks) (Atherton et al., 1990; Dias Tagliacozzo & Valio, 1994; Wohlfeiler et al., 2021). According to Alessandro et al. (2013), the early flowering (annual) in carrots is regulated by a single gene known as *vrn1*, which was identified as a dominant feature. Although annuals and biennials have different vernalization phases, both types have the same juvenile period (Alessandro & Galmarini, 2007). There is little information published regarding the juvenility and vernalization requirement of wild carrots, despite numerous studies on these requirements related to cultivated carrots. Due to the wide genetic diversity of wild carrots (Rong et al., 2010), their length of juvenility might vary more than cultivated carrots depending on the geographical locality (Nemeth, 1999). Moreover, wild carrots have low vernalization requirements, which is a key strategy for producing a large amount of seeds before extreme winter temperatures (Wohlfeiler et al., 2019). These observations indicate the importance of studying the life cycle of wild carrots via understanding the juvenility and vernalization requirements of wild carrots.

Wild carrot populations have shown a wide variety of life history behaviour such as annuals, biennials and perennials (de Jong et al., 2016; Mandel & Brunet, 2019). Furthermore, the geographical location and climate conditions are the key determinants of the wild carrot's life

cycle. This highlights the significance of researching wild carrot behaviour at the regional level (Kumarasamy et al., 2005; Wijnheijmer et al., 1989; Wohlfeiler et al., 2019). Furthermore, timely research of the life cycle of wild carrots is important for understanding plant adaptation and evolution under climate change. Also, studying the life cycle of wild carrots in a timely manner is crucial to comprehending how these invasive weeds evolve and adapt to changing climatic conditions. Meanwhile, the flowering synchrony of wild and cultivated carrots can be predicted when the life history of wild carrots is known at a particular climatic condition. This could help in avoiding undesirable hybridization between wild and cultivated carrots through implementation of timely weed management strategies, such as early detection and removal, and managing the wild carrots prior to the flowering to avoid synchronization with the flowering of cultivated carrots (Hauser & Shim, 2007). This emphasises the importance of studying the life cycle of wild carrots in the context of designing weed management techniques to reduce its spread (Van Etten & Brunet, 2017).

New Zealand supplies around 50 % of the world's carrot seeds, mainly at the request of international seed companies who contract New Zealand producers for the production of hybrid carrot seeds (Bhatia, 2023; Preece, 2023). Generally, hybrid carrot seed production comprises the controlled crossing between the selected male and female lines to obtain seeds with desirable traits, such as high yield, resistance to pests and diseases, and homogeneity (Broussard et al., 2017). This hybridization process mostly uses cytoplasmic male sterile (CMS) lines to avoid self-pollination in female plants, confirming that only pollen from the selected male line contributes to their fertilization (Simon, 2021). Furthermore, pollinators, such as honey bees, hoverflies, nectar scarabs, muscoid flies, and European Blue Blow Flies facilitate the pollen transfer from male to female line (Gaffney et al., 2018; Howlett, 2012). On the other hand, wild carrots also flower

adjacent to male carrot lines and act as pollen donors, which could deteriorate the cultivar purity of carrot seeds via undesirable hybridization with carrot female lines (Broussard et al., 2017; Mandel & Brunet, 2019). As a result, commercial carrot seed production sites have been threatened due to the emergence of wild carrots, especially in close proximity to the commercial carrot seed-producing sites (Godwin et al., 2024b).

Moreover, there is a major research gap in studies related to the flowering behaviour of wild carrots in New Zealand. Furthermore, several investigations on the juvenility (juvenility refers to the developmental stage during which carrot plants are insensitive to vernalization signals) and vernalization (exposure to cold necessary for flowering in some cultivars) responsiveness of cultivated carrots have been undertaken (Atherton et al., 1990; Wohlfeiler et al., 2021). However, no research has been done to study the interaction effect between different juvenility and vernalization of wild and cultivated carrots in New Zealand and internationally. Thus, this study's objectives are (i) to determine the interaction effects between juvenility and vernalization on flowering and floral characteristics of wild and cultivated carrots and (ii) to investigate the life cycle and floral morphology of wild carrots in New Zealand. This study will help to understand how the flowering pattern of wild and cultivated carrots varies under different juvenile and vernalization requirements. This study provides key insights for researchers, policymakers, seed industrialists, and growers to increase hybrid carrot seed production in New Zealand and globally by managing wild carrots to prevent genetic contamination.

6.2 Materials and methods

6.2.1 Plant materials and study site

A pot experiment was conducted at the Plant Growth Unit (PGU), Massey University in Palmerston North, New Zealand (40°22'41.1"S, 175°36'49.3"E) for a calendar year starting from 26 July 2022 to investigate the flowering phenology of wild and cultivated carrots in terms of the need for juvenility and vernalization requirements. The key reason for choosing male carrot lines and wild carrots for this study is that both can act as pollen donors to the female plants. Seeds of cultivated carrot (Male line No 27) was obtained from South Pacific Seeds Ltd. Wild carrot seeds were collected from Dairy One, a farm at Massey University, Palmerston North, New Zealand (40°22'31.0"S, 175°36'21.3"E) in May 2022. Seeds were air-dried under ambient conditions for 5 days, and debris was removed from the seed lot. The male line seeds and sorted wild carrot seeds were sealed in separate plastic boxes and stored at 5 °C and 50 % relative humidity (Zhao et al., 2022).

6.2.2 Crop establishment and husbandry

Wild and cultivated carrot seedlings were established in PVC pipes (Marley OPTIM® DWV Pipe SN6) that had a 50 cm height and a 10 cm diameter, filled with potting mixture (Wohlfeiler et al., 2021). The potting mixture consisted of a 3:1 ratio of soil and sand, constituting 80 % sand, 12 % silt, and 8 % clay (Yadav et al., 2021). Each pot was subsequently filled with 4 L of potting mixture and slow-release fertilizer 'Osmocot Exact Standard' at the rate of 4 g/L. This fertilizer provides a consistent supply of nutrients (15N-3.9P-9.1K+1.2Mg+ Trace elements) over an extended period (around 8-9 months). Garden nets were placed across the bottom of each pot to enhance the drainage of excess water after irrigation. The wild and cultivated carrot seeds were sown at a rate

of 3 seeds per pot. Additional seedlings were grown separately and transferred as needed to experimental pots at the three-unfolded true leaf stage (Wohlfeiler et al., 2022). Initially, manual irrigation was practised by using a spray lance with a seedling nozzle until seedling emergence. Thereafter, plants were irrigated at a rate of 4 ml/day/plant until they were moved to growth chambers (walk-in room with controlled temperature using air conditioning and heating used to provide vernalization temperature). A watering-can was used to irrigate the plants inside the growth chamber. Weekly manual weeding was carried out throughout the study period. Pesticides were sprayed in response to the pest and disease infestations, with no fixed frequency for spraying. Mit-e-mec[®] (Milbemectin, rate of active ingredient (ai)- 9.3 g/L) and Mavrik[®] (Tau-fluvalinate, ai rate- 240 g/L) were used to control the mite attack, and Attack[®] (Pirimiphos-methyl, ai rate- 475 g/L; Permethrin, ai rate- 25 g/L) and Carbendazim, ai rate- 500 g/L were sprayed to manage thrips and fungal infestation (carrot leaf blight), respectively.

6.2.3 Experimental design and treatment combinations

For the study, a Randomized Complete Block Design (RCBD) in a three-way factorial arrangement with four ($n = 4$) replications, along with five plants ($r = 5$) in each replication was used. The first factor was genotype (G) with two levels (wild carrot and cultivated carrot). The second factor was the juvenile period (J) with three levels (12 weeks, 8 weeks and 4 weeks). The third factor was vernalization (V) with three levels (12 weeks, 4 weeks and no-vernalization). Accordingly, eighteen treatment combinations (2 levels of $G \times 3$ levels of $J \times 3$ levels of V) were generated for this experiment. Thus, 360 plants (18 treatment combinations \times 4 replicates \times 5 plants per replicate), comprising 180 wild and 180 cultivated types, were established in total. The schematic diagram of the experimental schedule and treatment combinations is shown in **Figure 6.1**.

Year	2022																								2023						
Month	Jul	Aug					Sep					Oct					Nov					Dec					Jan				
Date	26	2	9	16	23	30	6	13	20	27	4	11	18	25	1	8	15	22	29	6	13	20	27	3	10	17	24	31			
Treatment Combinations	Juvenility treatment (J)												Vernalization treatment (V)																		
Cultivated carrots (G ₁)																															
G ₁ J ₁ V ₁	12-weeks (J ₁)												12-weeks (V ₁)												PV						
G ₁ J ₁ V ₂	12-weeks												4-weeks (V ₂)				PV														
G ₁ J ₁ V ₃	12-weeks												No-vernalization (V ₃)																		
G ₁ J ₂ V ₁						8-weeks (J ₂)							12-weeks										PV								
G ₁ J ₂ V ₂						8-weeks							4-weeks				PV														
G ₁ J ₂ V ₃						8-weeks							No-vernalization																		
G ₁ J ₃ V ₁									4-weeks (J ₃)				12-weeks										PV								
G ₁ J ₃ V ₂									4-weeks				4-weeks (V ₂)				PV														
G ₁ J ₃ V ₃									4-weeks				No-vernalization																		
Wild carrots (G ₂)																															
G ₂ J ₁ V ₁	12-weeks (J ₁)												12-weeks (V ₁)												PV						
G ₂ J ₁ V ₂	12-weeks												4-weeks (V ₂)				PV														
G ₂ J ₁ V ₃	12-weeks												No-vernalization (V ₃)																		
G ₂ J ₂ V ₁						8-weeks (J ₂)							12-weeks										PV								
G ₂ J ₂ V ₂						8-weeks							4-weeks				PV														
G ₂ J ₂ V ₃						8-weeks							No-vernalization																		
G ₂ J ₃ V ₁									4-weeks (J ₃)				12-weeks										PV								
G ₂ J ₃ V ₂									4-weeks				4-weeks				PV														
G ₂ J ₃ V ₃									4-weeks				No-vernalization																		

Figure 6.1 Schematic diagram of treatment combinations and experimental schedule; PV: Post-Vernalization

6.2.3.1 Juvenility treatment

Generally, the initiation of flowering can be influenced by the timing or age (juvenility) at which plants are shifted to floral inductive conditions (Cave et al., 2011). In this study, the length of the juvenile phase was divided into 3 levels to determine how the age of both wild and cultivated carrots has influenced their flowering behaviour and phenology (Atherton et al., 1990). In order to achieve the 12-week (J₁), 8-week (J₂), and 4-week (J₃) juvenile phases, wild and cultivated carrot seeds were sown in a glasshouse on 26 July, 23 August, and 20 September 2022, respectively (**Figure 6.1**). The 12-week treatment (J₁) was started at first, which is why it corresponds to the longest juvenile phase. The important reason for using a glasshouse in this experiment was to provide suitable controlled microclimate, including the temperature and photoperiod, for the

growth and development of plants during their juvenile phase. The plants were established at an average temperature of 20.25 °C in the glasshouse. Cool daylight fluorescent lights (Philips TLD 58w/865) were used in the glasshouse to provide the seedlings with a long-day photoperiod (16 hours of light and 8 hours of darkness) with the light intensities ranging from 140 to 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$ (**Table 6.1**).

6.2.3.2 Vernalization treatment

Vernalization is an important process in the induction of flowering in carrots, occurring after the juvenile phase (Liu et al., 2020). Therefore, the vernalization treatments (V_1 , V_2 , and V_3) were undertaken from 19 October 2022, following the juvenility treatments (**Figure 6.1**). Both the wild and cultivated plants from each juvenility treatment (J_1 , J_2 , and J_3) were categorized into three different groups to implement the vernalization treatment (V_1 , V_2 , and V_3). Thereafter, all the plants were transferred from the glasshouse to the growth chambers to provide different vernalization conditions for the plants. The plants belonging to the V_1 and V_2 treatments were maintained in growth chambers under low temperature (V_1 : 6.00 °C (mean temperature over 12 weeks), and V_2 : 7.05 °C (mean temperature over 4 weeks)) and short day photoperiod (8 h light/16 h dark; light intensity- 140 to 150 $\mu\text{mol m}^{-2} \text{s}^{-1}$) condition (**Table 6.1**) for 12-weeks and 4-weeks, respectively. Even though the minimum and maximum temperatures were the same for both V_1 and V_2 treatments, the mean temperature differed by 1 °C because the durations of the two treatments were different, where 12 weeks for V_1 and 4 weeks for V_2 . During these periods, plants were maintained in the same growth chamber, but the mean temperature was calculated over the entire duration (4 weeks and 12 weeks) of each treatment, which led to the temperature difference (**Table 6.1**). Following the completion of vernalization, plants belonging to V_1 and V_2 treatments

were gradually exposed to post-vernalization conditions with a mean daily temperature of 17.90 °C under long-day photoperiod (**Table 6.1**) from 10 January 2023 and 15 November 2022, respectively, until the end of the study. The plants belonging to V₃ (no-vernalization, control treatment) were maintained at a mean temperature of 17.29 °C under a long-day photoperiod, 16 h light (light intensity: 140 to 150 μmol m⁻² s⁻¹), and 8 h dark in separate growth chambers for the whole trial from 19 October 2022.

6.2.4 Sampling and measurements

Data on flowering percentage, days taken to flowering, overwinter survival percentage, height of floral stalk at flowering, total number of branches, and total number of umbels were collected in the glasshouse and growth chambers. Elongation of the first floral stem internode was used as an indicator to determine the flowered plants (Alessandro & Galmarini, 2007). Flowering was recorded on a daily basis throughout the trial. The percentage of flowering plants was calculated by using **Equation 1**, and the time taken for flowering from seed sowing was calculated. The survival percentage of plants after the vernalization treatment was calculated by using **Equation 2**. When the plants reached their end stage of flowering, the parameters such as the maximum height of floral stem (from base to tip of the primary umbel) and the total number of branches were recorded from all the plants (Noor et al., 2020). Moreover, the number of umbels per plant was recorded throughout the study to determine the total number of umbels at the end of the study. Plants that did not initiate a floral stem during the juvenile, vernalization, or post-vernalization phases were classified as non-flowering. Consequently, there was no data related to floral traits gathered from non-flowering plants during the study period.

$$\text{Percentage of flowered plants} = \left(\frac{\text{Number of flowered plants}}{\text{Total number of plants}} \right) \times 100 \rightarrow 1$$

$$\text{Survival percentage} = \left(\frac{\text{Number of survived plants after vernalization}}{\text{Total number of plants}} \right) \times 100 \rightarrow 2$$

6.2.5 Statistical analysis

A three-way Analysis of variance (ANOVA) was conducted with RStudio (version 2022.07.2 + 576) to assess the effects of the genotype (G), juvenility (J), vernalization (V) and their interaction on collected parameters. Tukey's post-hoc tests were carried out at a 5 % significance level ($p < 0.05$) to determine differences among the means for the various treatments considered.

Table 6.1 Growing conditions at different growth stages

Growth stages and treatments		Growth conditions (Wohlfeiler et al., 2022)						
		T _{min} (°C) ^a	T _{max} (°C) ^a	T _{avg} (°C) ^a	CV _t % ^b	Photoperiod ^c	Light intensity ^d	Location
Juvenility treatment	J ₁							
	J ₂	14.00	28.5	20.26	4.84 %	Long-day		Glasshouse
	J ₃						140 – 150	
Vernalization treatment	V ₁	5.13	12.11	6.00	25.23 %	Short-day	μmol m ⁻² s ⁻¹	Growth chamber
	V ₂	5.13	12.11	7.05	33.23 %			
	V ₃	14.37	18.84	17.29	13.81 %	Long-day		
Post-vernalization		13.15	19.13	17.90	14.51 %	Long-day		

Note: ^a Daily minimum (T_{min}), maximum (T_{max}), and average (T_{avg}) temperature were recorded using an electronic data logger

(DS1923 iButton®); ^b Coefficient of variation of temperature; ^c Long day- 16/8 h (day/night); Short day- 8/16 h (day/night); ^d Light intensity was measured using a light meter (LI-COR; Model LI-250)

6.3 Results and discussion

6.3.1 Flowering responses of wild and cultivated carrots to juvenility and vernalization period

The timing and success of flowering in *Daucus carota* species, including both cultivated and wild carrots, is influenced by juvenility and vernalization requirements (Wohlfeiler et al., 2022). The interaction effect between genotype, juvenile period and vernalization period was significant ($p < 0.05$) for the flowering percentage and time taken for flowering from seed sowing (**Figure 6.2** and **Figure 6.3**).

6.3.1.1 Flowering percentage

Flowering percentage is an important indicator of a carrot's reproductive capacity and broader adaptability to various environmental conditions (Loarca et al., 2024). Flowering percentage differed significantly ($p < 0.05$) among the treatment combinations. There was no flowering in cultivated carrots (G_1) that had been subjected to treatment V_2 (4 weeks of vernalization) and treatment V_3 (no vernalization). Furthermore, cultivated carrots that were exposed to 12 weeks of vernalization treatment (V_1) at 12 weeks ($G_1J_1V_1$), 8 weeks ($G_1J_2V_1$), and 4 weeks ($G_1J_3V_1$) of juvenile phase showed 100 %, 87.5 %, and 7.69 % of flowering, respectively (**Figure 6.2**). However, the 4-week juvenile treatment that results in a lower flowering percentage (7.69 %) cannot be considered due to the low seed formation in the context of commercial carrot seed production. As the juvenile age of cultivated carrots extended from 4 weeks to 12 weeks, the flowering percentage increased by around 92 % due to an increased vernalization response. This clearly suggests that the vernalization response is enhanced with the increasing juvenile age of cultivated carrots, achieving its peak at 12 weeks of plant age. These findings are consistent with the results of Atherton et al. (1990), who stated that the cultivated carrots (cv.

Chantenay Red Cored) younger than 6 weeks of juvenile age failed to demonstrate any vernalization response; as plants aged up to ten weeks, there was an increase in vernalization response and all of the plants flowered at 10 weeks due to the vernalization stimuli.

In addition, the findings from this study rationalise why cultivated carrots grown in New Zealand are biennial or late-flowering type, requiring around 12 weeks of vernalization at 5 °C to induce flowering (Alessandro & Galmarini, 2007). Similar findings were observed by Wohlfeiler et al. (2021), who found that the biennial carrots required lengthy cold exposure (11-12 weeks) compared with annuals (1-4 weeks) in order to induce flowering. The study also highlighted that the response to vernalization mainly relies on a range of genetic and environmental factors, as evidenced by different flowering responses of wild and cultivated genotypes of carrots to various chilling periods (12-week, 4-week, and no-vernalization). Moreover, Wohlfeiler et al. (2019) indicated that the *Vrn-A* and *Vrn-B* genes are important regulators in controlling the transition from vegetative stage to flowering in response to vernalization in carrot genotypes.

Furthermore, it is clear that the wild carrots in New Zealand have the ability to flower without vernalization ($G_2J_1V_3$, $G_2J_2V_3$, and $G_2J_3V_3$), emphasising the annual behaviour of wild carrots (Wohlfeiler et al., 2019). When the wild carrots entered ($G_2J_1V_1$, $G_2J_2V_1$, $G_2J_3V_1$, $G_2J_1V_2$, $G_2J_2V_2$, and $G_2J_3V_2$) into the overwintering phase (vernalization), they flower and set seed during the post-vernalization stage. Similar finding was reported by Mandel & Brunet (2019), who noted that the wild carrots that survived the winter flowered during the following summer. Based on this, it is clear that the age of the plant when entering vernalization influences its nature of life cycle, with the earlier establishment of wild carrots, especially prior to the winter, leading to a strong possibility of annual growth behaviour (Geoffriau et al., 2019).

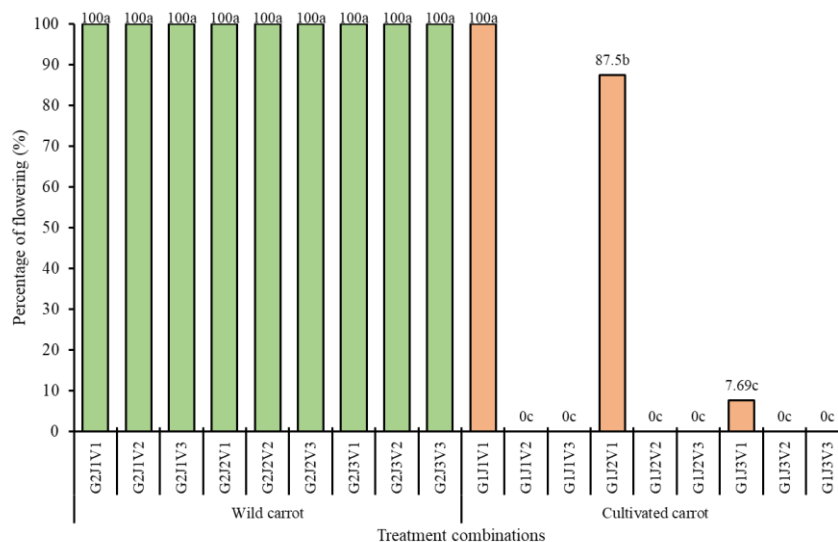


Figure 6.2 Flowering percentage of wild and cultivated carrots under different vernalization and juvenile period treatments. Data presented are means. Means with different lowercase letters are significantly different among the treatment combinations based on Tukey HSD method ($p < 0.05$). G, J and V represents the different genotype, juvenility periods, and vernalization periods, respectively.

6.3.1.2 Time taken for flowering

Understanding the flowering pattern and flowering time of wild and cultivated carrots is important in investigating the phenology of both subspecies of *Daucus carota* since flowering is one of the key growth stages that is closely related to the overall life cycle (Loarca et al., 2024). The results showed that the duration between sowing and flowering varied significantly ($p < 0.05$) across the treatment combinations. The longest time before flowering from sowing was recorded as ~236 days for G₁J₁V₁ treatment combination (**Figure 6.3**), which is the standard practice (12 weeks for juvenile phase and 12 weeks for vernalization) followed by most of the carrot seed producers. The reason for the decimal is that 236.25 days represents the mean from five replicates. The 236.25 days are divided into the juvenile stage (fixed at 84 days or 12 weeks), the vernalization stage (84 days or 12 weeks), with the remaining 68.25 days

allocated to the post-vernalization phase. This is why some values are given as whole numbers and others as decimals (**Figure 6.3**). Furthermore, wild carrots with a long juvenile phase but no vernalization ($G_2J_1V_3$) were the fastest to flower (~76 days), followed by wild carrots with, in addition, a short juvenile phase ($G_2J_3V_3$ with approximately ~78 days). The findings clearly indicated that the wild carrots require less time than the cultivated carrots for flowering, both in vernalization and in juvenile phases. This might be mainly due to the different life history strategies of wild and cultivated carrots in New Zealand, where the wild and cultivated carrots exhibit annual and biennial behaviour, respectively. The important reasons for differences in life history strategies of wild and cultivated carrots are genetics, relating to genes *vrn-A*, and *vrn-B*, which regulate the vernalization requirement, and environmental factors, such as latitude and habitat's resource quality (Mandel & Brunet, 2019; Wohlfeiler et al., 2019). However, when wild carrots are exposed to vernalization conditions for long periods (chilling the plants for 12 weeks at 5 ° C), floral induction is halted and only resumes after the completion of vernalization. As a result, the time taken to flowering is prolonged in some of the treatment combinations, such as $G_2J_1V_1$ (~189 days), $G_2J_2V_1$ (~158 days), and $G_2J_3V_1$ (~133 days) compared with wild carrots without a vernalization treatment, such as $G_2J_1V_3$ (~76 days), $G_2J_2V_3$ (~84 days), and $G_2J_3V_3$ (~77 days) (**Figure 6.3**). The rosette of wild carrots was present in treatment combinations $G_2J_1V_1$, $G_2J_2V_1$, and $G_2J_3V_1$ flowered post-winter conditions (vernalization), which indicated their behaviour as a winter annual. Conversely, wild carrots also flowered in the non-vernalized treatments such as $G_2J_1V_3$, $G_2J_2V_3$, and $G_2J_3V_3$, indicating under some environmental conditions wild carrots can behave as a summer annual. In short, wild carrots in New Zealand can be classified as winter annuals (seed germinates in autumn, rosette survives in winter, and flowering occurs in summer of the first year) and summer annuals (seed germinate in spring and flowering occurs in summer of the first year) (Mandel & Brunet, 2019).

Similar findings were reported by de Jong et al. (2016), who revealed that most of the wild carrots in the Netherlands have exhibited winter annual (38.9 %) and summer annual (36.8 %) behaviour. The key reasons for the bimodal (winter annual and summer annual) response strategy of wild carrots are origin and environmental factors. When the vegetative phase of wild carrots overlaps with winter, reproductive growth can be prolonged due to undesirable climatic conditions for flowering, resulting in the establishment of a winter annual. In contrast, if flowering happens in spring, it leads to the formation of a summer annual (Mandel & Brunet, 2019).

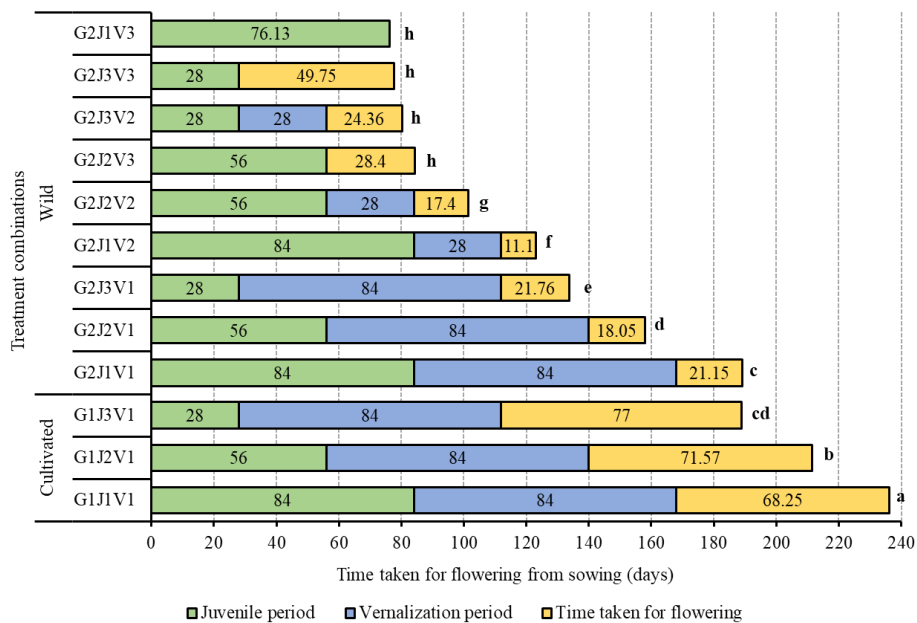


Figure 6.3 Time taken for flowering of wild and cultivated carrots under different vernalization and juvenile period treatments. Data presented are means. Means with different lowercase letters are significantly different at $P < 0.05$ (Tukey's post hoc tests). G, J, and V represents the different genotype, juvenility periods, and vernalization periods, respectively.

Figure 6.4 and **Figure 6.5** illustrate the relationship between the flowering percentage and the time taken for flowering from sowing. For cultivated carrots belonging to the treatment combination $G_1J_3V_1$, only 7.69 % of the cultivated carrots flowered at 189 days after the seed

sowing (or at 77 days after the vernalization treatment), when exposed to cold temperature for 12 weeks. Furthermore, because of 12 weeks' vernalization cultivated carrots in treatment $G_1J_1V_1$ and $G_1J_2V_1$, exhibited flowering percentages of 100 % and 87.5 % at 247 days and 221 days from the seed sowing (**Figure 6.4**). The key reason for the variation in achieving flowering of cultivated carrots is that the plants were exposed to the vernalization at different juvenile stages (J_1 -at 12 weeks, J_2 - at 8 weeks, and J_3 - at 4 weeks). Furthermore, wild carrots had the highest flowering percentage (100 %) in all the treatment combinations studied, with the time taken for flowering increasing with the length of juvenile and vernalization treatment. For instance, wild carrots that did not receive vernalization reached 100 % flowering at around 90 days, whereas wild carrots that received 12 weeks of vernalization achieved 100 % flowering between 150 and 230 days from seed sowing (**Figure 6.5**). Similar findings (Wohlfeiler et al. 2021) show that the time taken for flowering is influenced by the vernalization requirement of different carrot germplasms (including annual and biennials).

From the findings of this study, it is clear there is a high probability of overlapping flowering periods of wild and cultivated carrots in New Zealand. Since the wild carrots in New Zealand can behave as winter annuals and summer annuals, the flowering phase of cultivated carrots is likely to coincide with the flowering period of wild carrots. For instance, if the rosettes of wild carrots withstand the winter, i.e., behave as winter annuals, and initiate flowering in spring/summer, as shown in treatment combinations $G_2J_1V_1$, $G_2J_2V_1$, and $G_2J_3V_1$, the flowering period of cultivated carrots could overlap with wild carrots. In addition, if the wild carrots germinate in the spring and flower in summer, as a summer annual, as observed in treatment combinations $G_2J_1V_3$ (without winter survival), they could overlap the flowering season of cultivated carrots (de Jong et al., 2016). Consequently, there could be a significant threat of contamination of commercial carrot seeds via pollen flow when the wild carrots are established adjacent to the carrot seed crops (Godwin et al., 2024b). Given the diverse flowering pattern

of wild carrots, it is critical to manage the wild carrots prior to flowering to avoid undesirable pollen flows and ensure the production of genetically pure carrot seeds (Rome & Lucero, 2019).

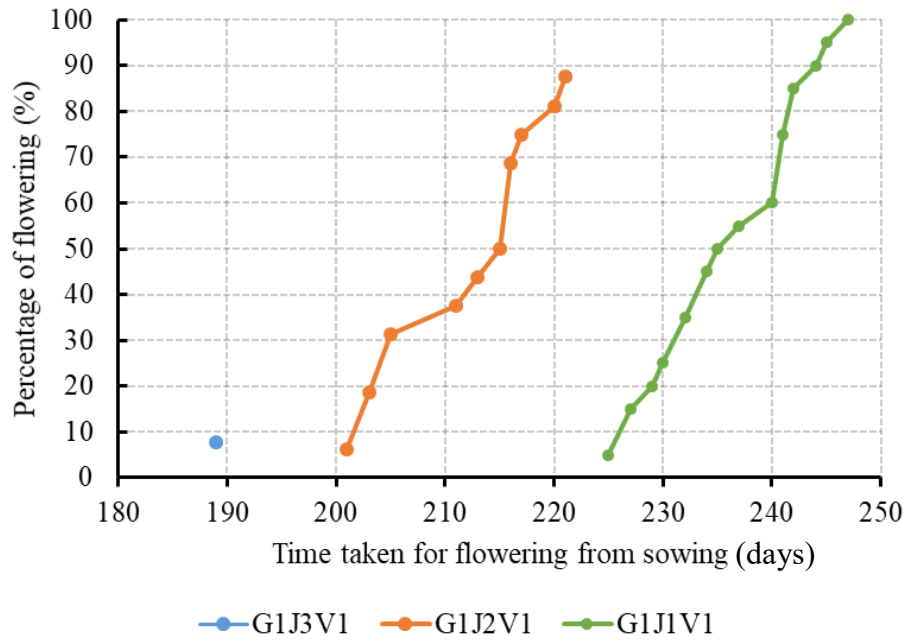


Figure 6.4 Relationship between percentage of flowering and time taken for flowering from sowing in the cultivated carrots with 12-week (V_1) vernalization and different juvenile periods (J_1 : 12 weeks, J_2 : 8 weeks, and J_3 : 4 weeks), G, J and V represents the different genotype, juvenility periods, and vernalization periods, respectively.

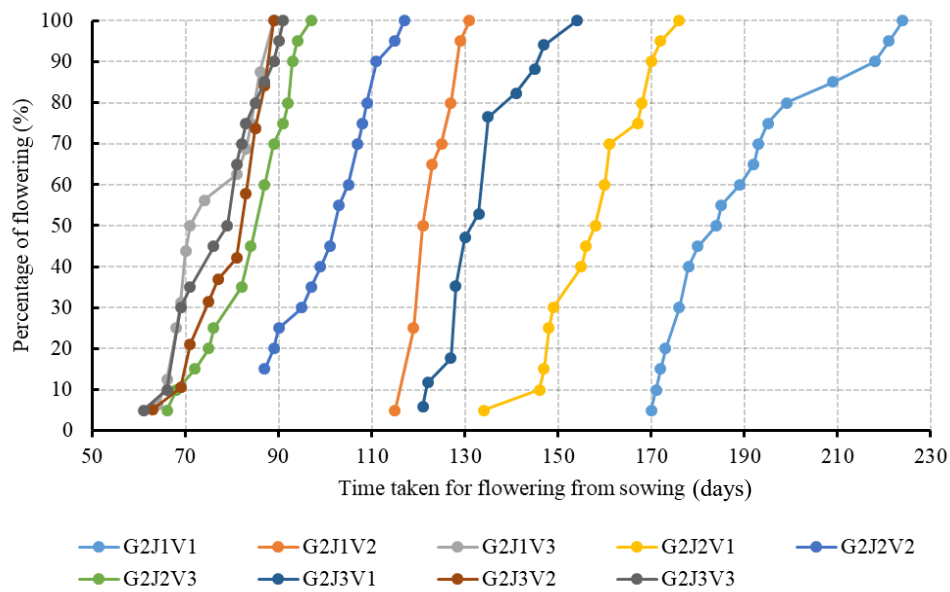


Figure 6.5 Relationship between percentage of flowering and time taken for flowering from sowing in the wild carrots with different vernalization (V_1 : 12 weeks, V_2 : 4 weeks, and V_3 : 0 weeks) and different juvenile periods (J_1 : 12 weeks, J_2 : 8 weeks, and J_3 : 4 weeks), G, J and V represent different genotype, juvenility periods, and vernalization periods, respectively.

6.3.2 Survival of wild and cultivated carrots during vernalization treatments

Controlling wild carrots prior to the overwintering stage is important, as they start to flower and proliferate, making them increasingly problematic (Van Etten & Brunet, 2017). Therefore, understanding the effect of different juvenile phases and vernalization conditions on the survival of wild and cultivated carrots is key to assessing their ability to survive over the winter and formulating weed management strategies based on their survival nature. A significant interaction effect between genotype and juvenility period ($P < 0.05$) was detected in relation to survival percentage during vernalization (overwinter survival). Comparatively, wild carrots demonstrated a higher rate (94.9 % - 100 %) of overwinter survival than cultivated carrots (66.1 % - 98.3 %) in New Zealand (**Figure 6.6**). This implies that wild carrots are more adaptable to winter conditions, which could be due to their natural adaptation processes. Specifically, over

time, wild carrots have evolved through natural selection to develop characteristics that enhance their survival in colder climates. According to the results, 12-week-old wild and cultivated carrot plants had higher winter survival rates, compared with 4-week-old seedlings by 5.1% (wild) and 32.2% (cultivated), respectively. Furthermore, the results of this study indicate that the winter survival percentage of wild carrots was higher when the plant's juvenile age was higher at the time of transitioning into the overwintering phase. This implies that older plants (12 weeks old) are more resilient to winter conditions, whereas younger plants (4 weeks old) are more susceptible to chilling conditions. This could be due to the underdeveloped physiological parts and root systems of younger plants compared with older plants (Lubbe et al., 2021). The plants might have died as a result of cold stress or low temperature injury. Plants with shorter juvenile periods (4 weeks old) and some 8-week-old plants may have had difficulty undergo vernalization conditions due to weak vegetative development. However, susceptibility to low temperature injury may vary between different cultivated carrot lines, suggesting an additional study to assess genotype-specific responses to vernalization and cold stress. Moreover, winter temperatures will probably rise with global warming, which could speed up the spread of wild carrots due to their strong survival nature over the winter (Van Etten & Brunet, 2017). As a consequence of climate change, winters are becoming gradually warmer in New Zealand (Ministry for the Environment & Stats NZ, 2020). As a result of higher overwinter survival rates and the favourable conditions caused by warmer winters, the threat wild carrots pose to carrot seed production in New Zealand in the future, will increase.

6.3.3 Floral characteristics of wild and cultivated carrots

Identifying the floral characteristics of wild and cultivated (especially male lines) is important for understanding how these traits influence competitive advantages in regards to the attraction of pollinators since the wild and cultivated carrots have the capacity to attract the same

pollinators (Howlett et al., 2015; Lamborn & Ollerton, 2000; Mandel & Brunet, 2019). The findings related to number of umbels, height of floral stalk, and number of branches are presented in **Figure 6.7**.

The interaction effect between juvenility and vernalization was significant ($p < 0.05$). Therefore, the floral traits of wild and cultivated carrots were assessed separately. The findings indicated that the wild carrots not exposed to vernalization (V_3) produced taller floral stalks and more umbels and branches than wild carrots grown under other treatment combinations (juvenility \times vernalization), except for the number of branches produced under J_1V_3 . Moreover, increasing the length of cold exposure from 4 to 12 weeks significantly ($p < 0.05$) affected the floral traits of wild carrots that were exposed to vernalization at the age of 12 weeks (J_1) and 8 weeks (J_2) by reducing the number of umbels, height of the floral stalk, and number of branches. This indicates that prolonged cold exposure might affect the reproductive growth of wild carrots. Based on these facts, as temperatures rise wild carrots showing summer annual behaviour will become more problematic than those with winter annual behaviour in the context of weed management and attraction of pollinators in New Zealand. Comparatively, wild carrots have produced a higher number of umbels and branches, and taller floral stalks than male lines of cultivated carrots (except floral stalk height in J_1V_1), which can stimulate the attraction of pollinators (**Figure 6.7**). Similar findings were reported by Koul et al. (1989), who noted that the wild carrots produced more umbel orders and flowers than cultivated carrots. In general, higher umbel counts attract pollinators to forage plants more frequently due to the increased floral density (Thomson, 1988). In addition, Gonzalez et al. (2018) observed that the height of floral stalk (umbel height) of wild carrots has a significant influence on the attractiveness of the pollinators. Similar findings were reported by Fornoff et al. (2017), who stated that flower height is positively correlated with the richness of species and frequency of insect visitations.

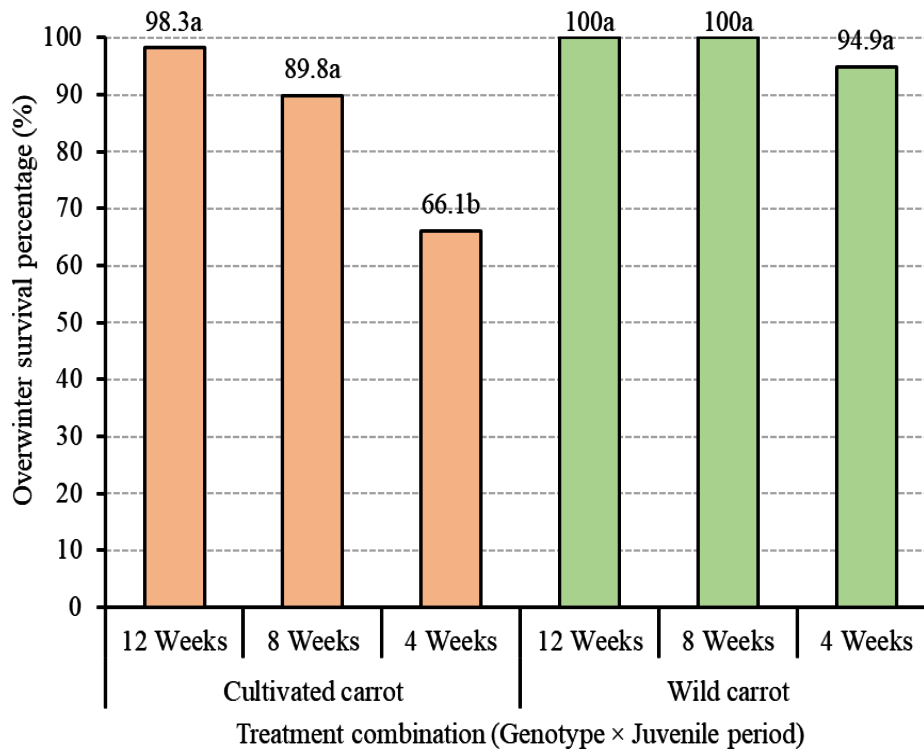


Figure 6.6 Overwinter survival percentage (%) of wild and cultivated carrots under different juvenile period treatments. Data presented are means. Means with different lowercase letters are significantly different among the treatment combinations based on Tukey’s method ($p < 0.05$).

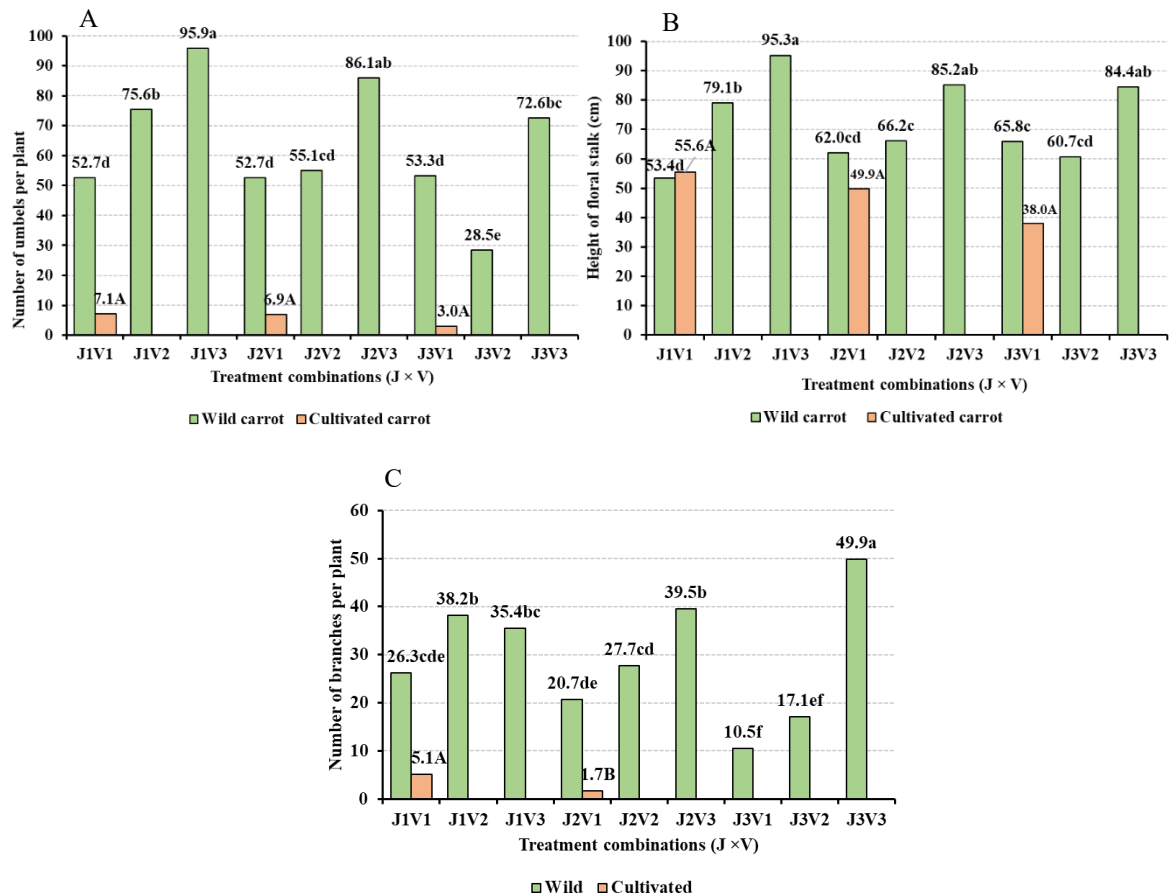


Figure 6.7 (A) Number of umbels, (B) height of floral stalk, and (C) number of branches of wild and cultivated carrots under different treatment combinations. Data presented are means. Means with different lowercase and uppercase letters are significantly different among the treatment combinations based on Tukey’s method ($p < 0.05$).

6.4 Conclusions

In conclusion, the duration of the juvenile stage (plant age), vernalization, and their interactions had a significant effect on the flowering responses of wild and cultivated carrots. In regard to commercial carrot seed production in New Zealand, the requirement of 12 weeks for vernalization emphasises the biennial nature of the commercially grown carrot cultivars, as they require a prolonged chilling period to transition from the vegetative to the reproductive phase. In contrast, wild carrots exhibit greater flexibility in their life cycle, flowering across all treatment conditions, even in the absence of vernalization. This adaptability permits wild

carrots to establish as either winter annuals or summer annuals in New Zealand, showing their capacity to thrive in different environments. The ability of wild carrots to flower without vernalization and their higher overwintering survival rates make them a persistent and potentially growing threat to the genetic purity of commercial carrot seeds. In addition, the projected effect of climate change, especially warmer winters, will further facilitate the overwinter survival of wild carrots in New Zealand, necessitating more aggressive and timely weed management strategies. Meanwhile, wild carrots have a more competitive advantage over male lines of cultivated carrots in attracting and rewarding pollinators due to the development of more umbels, branches and taller floral stalks. In the context of commercial carrot seed production, wild carrots must be controlled immediately after the winter to avoid the overlapping flowering periods of wild and cultivated carrots. The findings of this study significantly enhance the understanding of the life history strategies of wild and cultivated carrots. These insights are important for designing timely weed management practices to ensure the production of genetically pure commercial carrot seeds in New Zealand and other seed-producing regions.

Chapter 7: General discussion

7.1 Introduction

New Zealand produces about 50 % of the global carrot seed supply, making the carrot seed industry an important contribution to the New Zealand economy (Preece, 2023) as well as globally important for supply of carrot seed for production of carrot crops. There is a high global demand for premium carrot seeds since the market for carrot growers is expanding significantly along with the rising consumption of carrots (Simon, 2019b). While carrot seed production in New Zealand is primarily driven by contracts with global seed companies, these contracts enable New Zealand to support the growing global demand for carrot seeds. Most of the carrot seed production is based in the Canterbury region of the South Island. However, there is interest in extending the seed production in Hawke's Bay region due to the presence of a favourable climate and geographical features for carrot seed production (Bhatia, 2023). Although there are several long-standing challenges that affect carrot seed production, such as poor pollination, soil-borne pathogens (*Alternaria* sp disease), and seasonal yield variability, the industry has identified climate change and infestation of wild carrots adjacent to the carrot seed production sites as two emerging constraints (Broussard et al., 2017). Both challenges can significantly impact the quantity and quality of the carrot seeds. As a result of climate change, the production sites may be forced to shift to climatically favourable locations, where wild carrot infestation is prevalent. When the wild and cultivated carrots are located nearby and flower simultaneously, the pollen flow from wild to cultivated carrot is possible, which could potentially contaminate cultivar purity (Mandel et al., 2016). In the New Zealand context, only few studies have been conducted to address these two key constraints for expanding carrot seed production in New Zealand (Bhatia, 2023; Broussard et al., 2017).

To address the identified research gaps, the studies of this thesis were primarily conducted to investigate the impact of temperature and precipitation on performance of carrot, and to compare and understand the phenology of wild and cultivated carrots in the context of formulating timely weed management strategies. The rationale of this research is to alleviate these constraints and ensure the sustainability and quality of carrot seed production in New Zealand.

The work of this doctoral thesis consisted of a statistical modelling study (Chapter 3), a temperature gradient plate experiment (Chapter 4), a glasshouse experiment (Chapter 5), and a glasshouse-growth chamber experiment (Chapter 6). The impact of temperature and precipitation on carrot seed yield was studied in Chapter 3 via a panel data analysis. Whereas the effect of temperature on seed germination, one of the most sensitive stages to climate change, of wild and cultivated carrot was discussed in Chapter 4 by using thermal time modelling. The glasshouse and growth chamber experiments were conducted at the Plant Growth Unit (Massey University) to compare and investigate vegetative growth (Chapter 5) and reproductive growth (Chapter 6), including flowering behaviour and floral characteristics of wild and cultivated carrots. Chapter 5 further discussed the incorporation of different weed management strategies to control wild carrots in the context of growth stages. The relationship between the morphological traits of above and below ground parts of wild and cultivated carrots was further investigated in Chapter 5. Whereas Chapter 6 demonstrated the combination effects of different lengths of vernalization and juvenile stages on flowering behaviour and life history strategies of both wild and cultivated carrots. The importance of understanding the life history strategies in the context of pollen flow from wild to cultivated carrot was further studied in Chapter 6.

7.2 Key findings from this thesis

7.2.1 Carrot seed production in New Zealand will be impacted by subsequent climate change (Chapter 3)

A panel data modelling (Chapter 3) was carried out by using time series (2005-2022) and cross-sectional (28 different locations from Canterbury and Hawke's Bay region) to study the impact of maximum and minimum temperature, and rainfall during the juvenile, vernalization, floral development, and flowering and seed production phases on the production of carrot seeds. Findings validated that the temperature ranges between 8.15 °C and 19.30 °C during the time of juvenile stage have a positive influence on seed germination and root development in carrot-growing regions in New Zealand. Moreover, the results indicated that vernalization occurred from June to August, coinciding with a mean temperature of about 7 °C, this temperature is advantageous for the vernalization and, consequently, flower development. Furthermore, the climatic models indicated that the minimum and maximum temperature in carrot seed producing regions have been increasing considerably since 2005 throughout the growing cycle (13 months). Precipitation has shown a decreasing and an increasing trend during the vegetative and reproductive growth phases of carrots, respectively. The highest rate of variations in maximum and minimum temperature, and precipitation were reported during the vernalization phase (+0.254 °C/ year), floral development phase (+0.18 °C/ year), and juvenile phase (-6.508 mm/ year), respectively. The results from the marginal effect analysis indicated that the increasing precipitation was unfavourable to the seed yield throughout the phenological stages, except during vernalization. The highest significant marginal effects on carrot seed yield were observed during vernalization for minimum temperature (a 1 °C increase reduces yield by 187.724 kg/ha) and maximum temperature (a 1 °C increase raises yield by 132.728 kg/ha), while precipitation had the greatest impact during flowering and seed development (a 1 mm increase

reduces yield by 1.745 kg/ha). Even though carrot seed crops in Canterbury are irrigated, changes in rainfall patterns remain significant due to their influence on water availability and irrigation efficiency. These findings reported in Chapter 3 concluded that the degree to which temperature and precipitation affect carrot seed yield depends on the various phenological stages and on whether minimum or maximum temperature is considered. These findings highlight that climate change, with its expected increases in temperature and altered precipitation patterns, could significantly constrain carrot seed production by intensifying the sensitivity of key phenological stages to environmental conditions, emphasizing the significance for developing climate-resilient seed production strategies, including varieties better adapted to the new production environment.

7.2.2 Seed germination of wild and cultivated carrots can be affected by extreme temperature conditions (Chapter 4)

In Chapter 4, the impact of temperature (7 °C - 41 °C) was determined on the seed germination of wild and cultivated carrots. The findings indicated that the temperature, genotypes, and their interactions significantly ($p < 0.05$) affect the germination percentage (FGP), mean germination time (MGT), and time required for 50 % germination (T_{50}) of No 27 male line and No 27 female lines of cultivated carrots, and wild carrots. The highest percentage of germination was reported at temperatures of 20 °C for cultivated carrots, including male (98 %) and female (97 %) lines, and 21 °C for wild carrots (87 %); however, these differences were not statistically significant ($p > 0.05$). Furthermore, seed germination was completely inhibited at temperatures above 35 °C for wild carrots, 36 °C for the male line, and 37 °C for the female line. The climate change estimations for the Hawke's Bay and Canterbury region in New Zealand indicate that rising temperature is likely to increase the germination rates of wild and cultivated carrots, including male and female lines. As a result, the wild carrot infestation will

be increased in major carrot seed-producing regions in New Zealand, particularly when wild carrots are present in surrounding area. This can negatively affect the carrot seed production via undesirable hybridizations. Therefore, it is important to formulate appropriate weed management strategies to control the wild carrot infestations.

7.2.3 Wild carrots must be controlled before 9–11 leaves stage (Chapter 5)

In order to avoid unwanted pollinations, wild carrots must be controlled prior to the flowering. The findings from Chapter 5 indicated that the wild carrots must be controlled before 9 - 11 leaves stage, because the root and shoot growth becomes more rapid after 8 weeks of the juvenile stage (9 - 11 leaves stage). Once the wild carrot begins producing more foliage and lengthy roots, especially after 9 - 11 leaves stage, the weed management becomes problematic. Correlation analysis from chapter 5 indicated positive and significant ($p < 0.05$) correlations between above and below-ground morphological traits of both wild and cultivated carrots. To further facilitate, the Power regression models were identified, based on higher R^2 and lower $RMSE$, as potential models that can be used to predict the vegetative growth of wild and cultivated carrots, including shoot and root systems. These findings are useful for making decisions on the growth of root system, executing appropriate weed management strategies to control wild carrots and expanding the production locations, thereby enhancing the resilience of carrot seed production systems to withstand the impacts of climate change.

7.2.4 Cultivated carrots have shown a biennial nature in the context of seed production, whereas wild carrots can establish themselves as either summer annual or winter annual in New Zealand (Chapter 6).

In Chapter 6, the floral behaviour and life history strategies of wild and cultivated carrots have been studied in the context of New Zealand. The findings of this chapter indicated that the

interactions between the genotype, juvenility and vernalization periods had a significant ($p < 0.05$) impact on the flowering behaviour of both wild and cultivated carrots. Vernalization requirement for the cultivated carrot is intense, required 12-weeks, under New Zealand conditions, which emphasizes the biennial nature of the cultivated carrots in the context of seed production. However, the wild carrots have flowered under all the treatment combinations, illustrating their wide life history strategy. Furthermore, the overwintering survival of wild carrots ranged from 94.9 % (at 4 weeks J₃) to 100 % (at 12 weeks J₁) is comparatively higher than cultivated carrots, which ranged from 66.1 % (at 4 weeks J₃) to 98.3 % (at 12 weeks J₁). This highlights their ability to perform as a winter annual and as a summer annual. Comparatively, wild carrots have the capacity to produce higher umbels (by 93 %) and branches (by 90 %), and taller floral stalks (by 42 %) than No 27 male lines of cultivated carrots (a tall variety), which allows the wild carrots to compete with male cultivated carrots when attracting and rewarding pollinators.

7.3 Practical importance of the findings to the carrot seed industry

The findings from chapter 3 suggest that the phenological phases of carrot seed crops, such as juvenile phase, vernalization phase, floral induction phase, and flowering and seed development phase, show varying degrees of vulnerability to maximum, and minimum temperatures, and precipitation. As a result, it is important to formulate and adapt phenological stage-specific climate change strategies by the carrot seed growers to cope with projected climate change in New Zealand. According to the findings of chapter 4, seed germination rates of wild and cultivated carrots, including male and female lines, are likely to increase along with projected increment in autumn and spring temperatures in Hawke's Bay and Canterbury regions of New Zealand. Even though soil temperature directly affects germination, atmospheric temperature was used in this study due to its strong correlation with top topsoil layer temperatures and its broader accessibility in climate projections. As a result of rapid

germination of wild carrots, the infestation can be a serious threat in these regions. Furthermore, the wild carrot infestation is projected to become more vulnerable in Canterbury regions compared with Hawke's Bay regions under RCP 8.5 scenario. In addition, the findings of Chapter 4 on the cardinal temperature requirements of male and female lines of cultivated carrot seed germination are vital for the carrot seed industries, as they can make informed decisions on optimal sowing time. The results of chapter 5 stated that the appropriate weed management practices, such as hoeing, tilling, hand pulling, or herbicide spraying, should be executed before 9–11 leaf stages occur in wild carrots. Furthermore, this study (Chapter 5) also provides information for carrot seed growers and stakeholders, facilitating in decision-making and the development of region-specific weed management strategies to control wild carrot infestations and prevent its seed production. Wild carrots can be established as a summer annual and winter annual in New Zealand. As a result, there is a high possibility of synchronized flowering patterns of wild carrots with cultivated carrots. These insights are important for designing timely weed management practices to ensure the production of genetically pure commercial carrot seeds in New Zealand and other seed-producing regions.

7.4 Recommendations for future studies

To supplement the insights presented in this doctoral study, there are various research gaps requiring future investigation and are summarized in this section.

1. Panel data study may be expanded beyond the current panel data study by using data related to climatic factors, like soil temperature and light intensity, and management practices, such as usage of fertilizer, pesticide, and other farm inputs. This will facilitate to improve the accuracy of climate-resilience production models.
2. Conducting further germination assessments with a wider range of wild carrot and cultivated carrot genotypes from different geographical locations, incorporating soil

temperature conditions, to identify the adaptability of genotypes to new production locations.

3. Germination studies are required to determine the underlying factors contributing to lower seed germination in wild carrots, with a focus on domestication effects, seed dormancy, and environmental adaptations.
4. Assess pollen viability of wild and cultivated carrot at a range of temperatures and over time.
5. Re-assess the isolation distance requirement of wild carrot from cultivated carrot seed production sites to avoid pollen flow from wild to cultivated carrots and vice versa to avoid development of more persistent wild carrots.
6. Undertaking a field survey to develop spatial distribution map of wild carrot infestation in major carrot seed producing regions in New Zealand. This is important for identifying wild carrot infested areas for undesirable hybridization and can facilitate decision-making when selecting locations for future carrot seed production.
7. Identifying effective combinations of herbicides and other weed management strategies to control wild carrots (based on their phenological stage) infesting areas adjacent to cultivated carrot seed crops.

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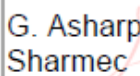
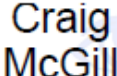
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Name and title of main supervisor:	Craig McGill		
In which chapter is the manuscript/published work?	4		
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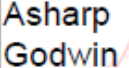
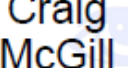
Student name:	Asharp Godwin		
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