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Review

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

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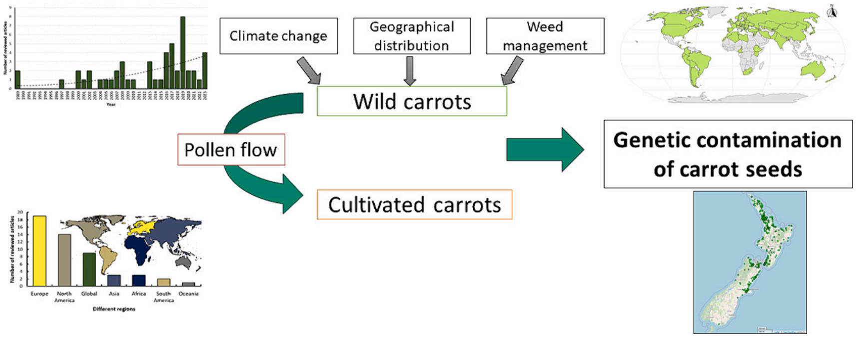
HIGHLIGHTS

- 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.

GRAPHICAL ABSTRACT



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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 %).

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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.

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 and 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 and 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 and 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 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) 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 and 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 and 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 and Harrison, 1966; Magnussen and 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, 2022). 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., 2019b; 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 and 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. Material and methods

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 Fig. 1. 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).

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 and 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.

3. Results and discussion

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 Fig. 2. 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.

The continent-based spatial distribution of the reviewed articles is shown in Fig. 3A. The results of this literature search showed wild carrots have spread globally except to the region of Antarctica. European colonization and the importation of hybrids (wild × cultivated) with cultivar seeds are the important causes for the introduction of wild carrots to new geographical locations (Iorizzo et al., 2013; Magnussen and 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

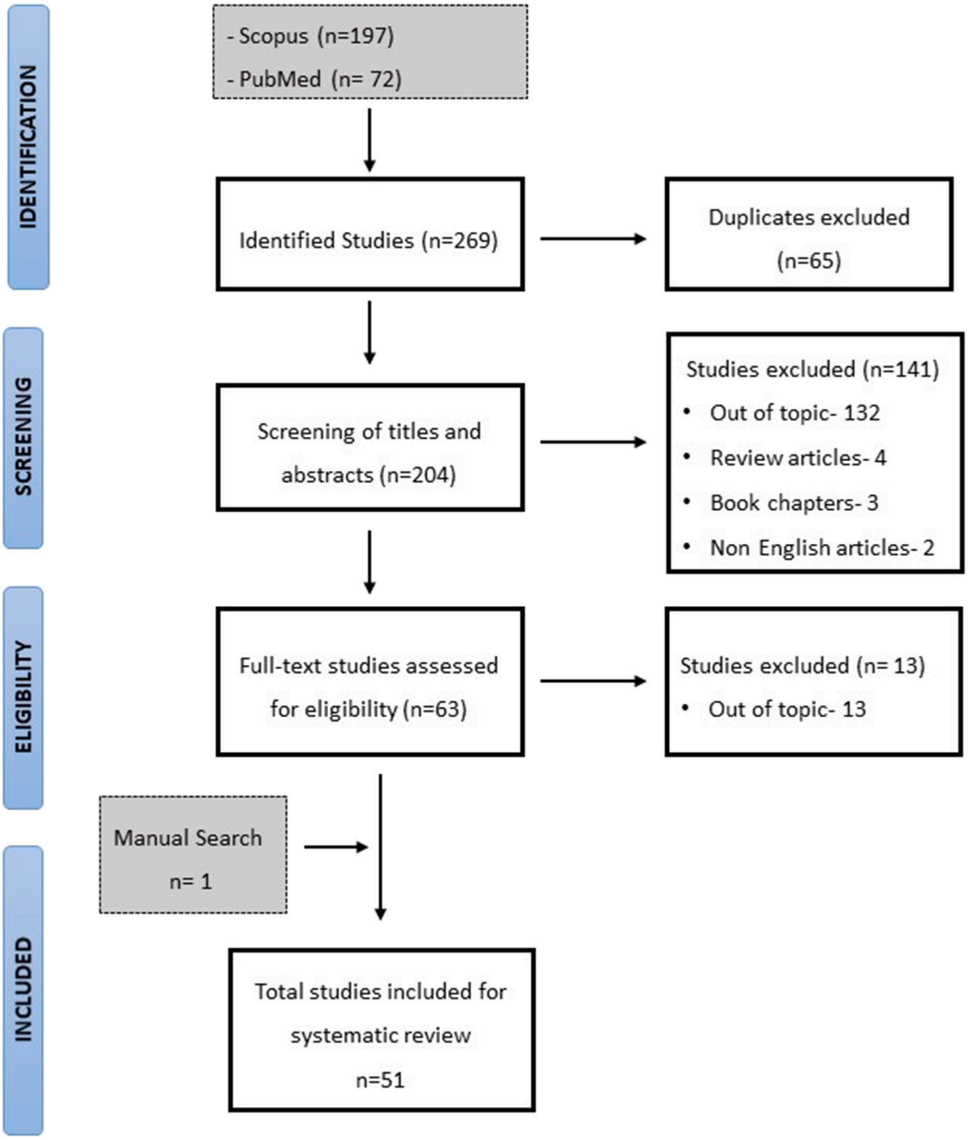

Fig. 1. Flow diagram for review process and selection of articles.

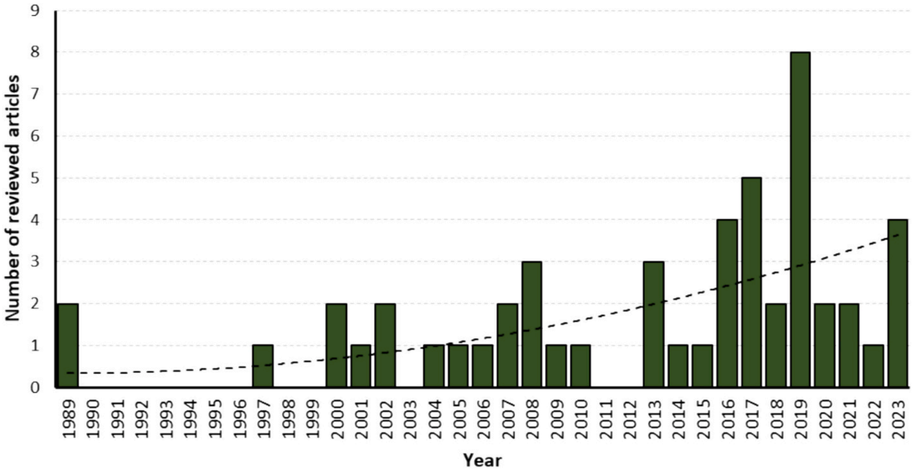

Fig. 2. Number of reviewed articles ($n = 51$) published by year.

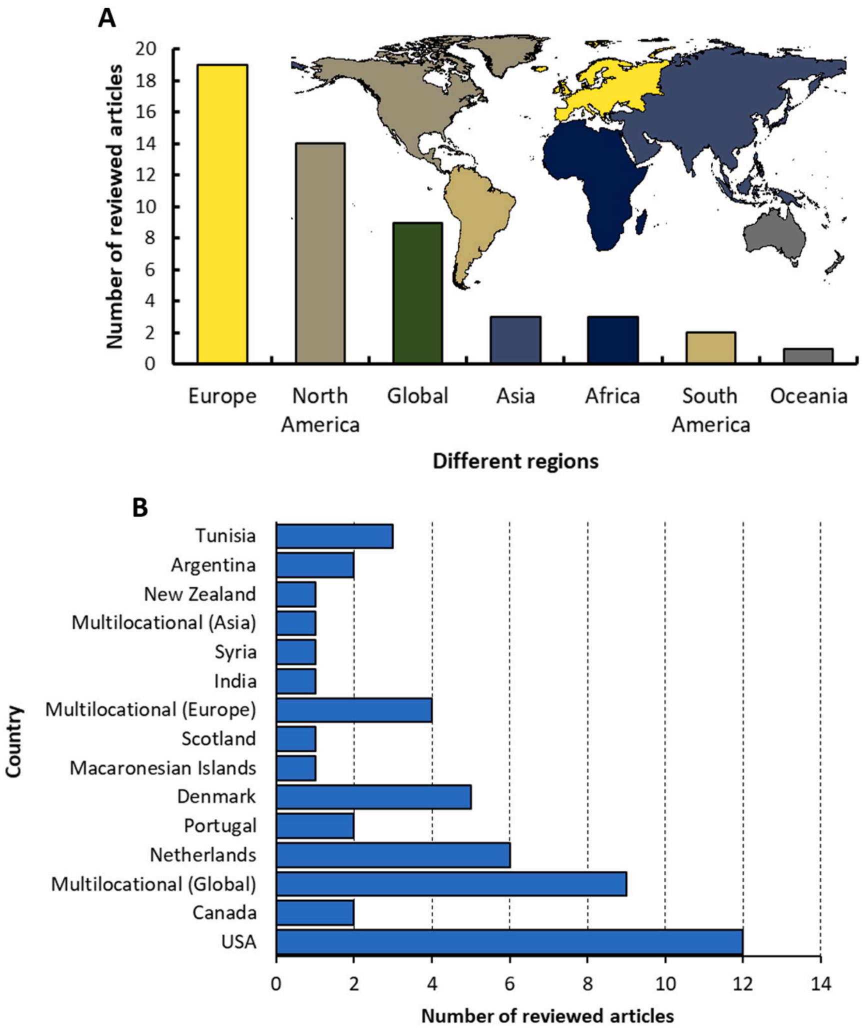

Fig. 3. Geographical coverage of reviewed articles (n = 51); **A,** based on continents and **B,** based on countries.

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 (Fig. 3B): 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).

3.2. *Wild carrots and their effect on quality carrot seed production*

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 lesser 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 and Simon, 2019; Mezghani et al., 2019b; 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 79,686) to the increased extreme saline conditions. The numerical value next to the country represents the seed bank accession number of *Daucus carota*. Wild carrots found in a coastal environment (England 79,686) performed better under saline conditions than the wild carrots inland (Azerbaijan 769,446), suggesting that the adaptability to the saline environment may depend on the provenance (location) of the wild carrot (Bickler et al., 2019).

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 *DcAOX1* 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 *DcAOX1* to identify the hotspots of carrot crop wild relatives (CWR) across Europe. They found variation in *DcAOX1* 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 *DcAOX1* 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. (2019b), 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 and Brunet (2017) 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., 2019a).

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.

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 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 and 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). This is further supported by the findings of Ibañez and Camadro (2015), who 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 carrot 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 and 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 and Bjørn, 2001; Hauser and 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

Table 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 and 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 and 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 and 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 and Camadro (2015)

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 <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 and 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 and Bjørn, 2001; Hauser and 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 and 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 non-marketable (Magnussen and 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 and Shim, 2007). Due to this, breeders and seed manufacturers attempt to avoid pollen flow from wild to cultivated carrots (Mandel et al., 2016; Shim and 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 manufacturers face difficulties in promoting their products and sustaining customer satisfaction.

3.2.3. *Spatial distribution of wild carrots*

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 (Fig. 4). 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, results of this review confirmed that wild carrots densely populated temperate climatic regions due to its adaptive nature (Hernández et al., 2023). Based on the geographical distribution of wild carrots (Fig. 4), it is clear that this weed is less common in African and south-east 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.

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 (Fig. 5A). 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 (Fig. 5B). 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

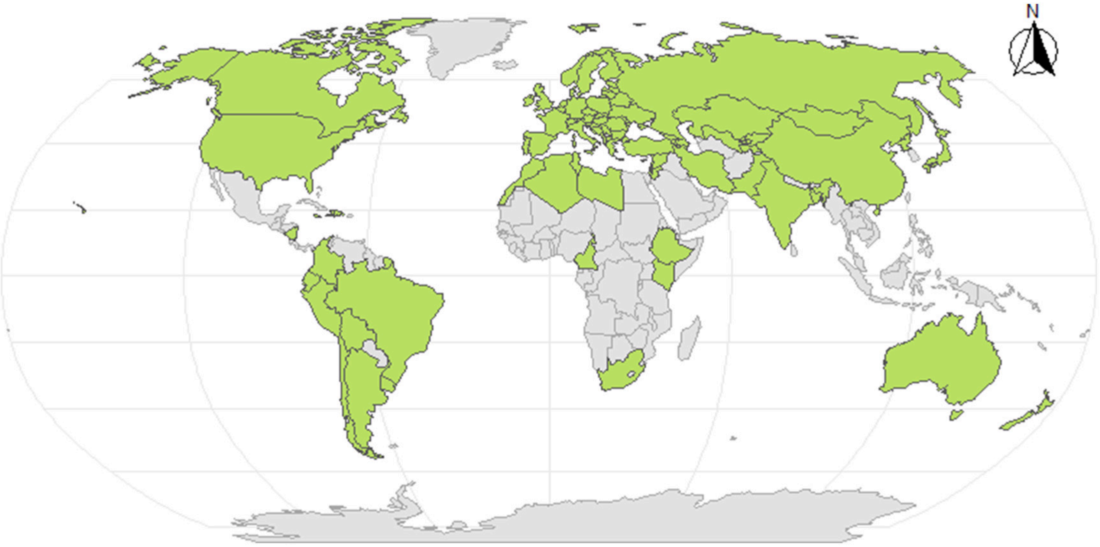

Fig. 4. Map demonstrating the global wild carrot distribution based on reviewed articles ($n = 51$) and data collected from iNaturalist.

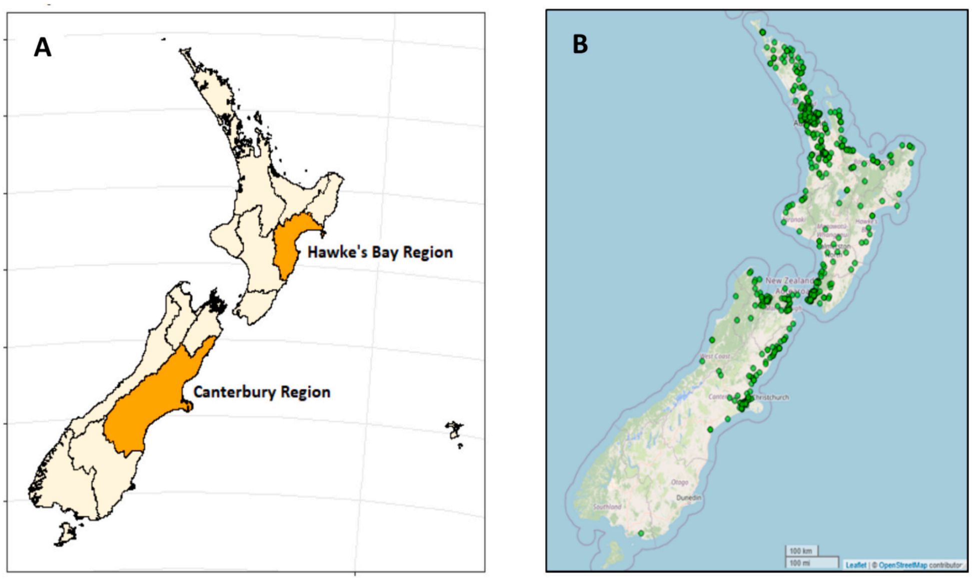

Fig. 5. **A**, Major carrot seed producing regions in New Zealand and **B**, Wild carrot invaded locations in New Zealand (OpenStreetMap contributors, 2017).

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 and 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.

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 and 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 and 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 and 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.

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). 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, the application of chemical spray is also an effective tool that can be used to control the 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

Table 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
		Acetochlor + dichlormid	1793 + 309 g ai/ha		
		Cyanazine	3026 g ai/ha		
		Linuron + Chlorimuron	557 + 31 g ai/ha	–	Stachler and Kells (1997)
		Metribuzin + Chlorimuron	336 + 32 g ai/ha		
		Atrazine + mesotrione + S-metolachlor	561 + 150 + 1504 g ai/ha		
	Germination OR early emergence	Atrazine + mesotrione + S-metolachlor	1122 + 300 + 3008 g ai/ha	Canaan fir (*Abies balsamea* var. *phanerolepis*) - POST	
Pre-Emergence		Hexazinone + sulfometuron methyl	289 + 27 g ai/ha		
		Hexazinone + sulfometuron methyl	480 + 46 g ai/ha		Aulakh (2020)
		Bentazon	1121 g ai/ha		Stachler and Kells (1997)
		Cyanazine	2212 g ai/ha	–	
		Picloram +2,4-D	0.23 + 0.84 kg ai/ha		
		Picloram +2,4-D	0.30 + 1.12 kg ai/ha		
		Triclopyr + clopyralid	0.96 + 0.32 kg ai/ha		
		Triclopyr + clopyralid	1.26 + 0.42 kg ai/ha	Orchardgrass (*Dactylis glomerata* L.) and tall fescue (*Festuca arundinacea*)	Bradley et al. (2004)
	Seedling	2,4-D + triclopyr	2.20 + 1.12 kg ai/ha		
		Saflufenacil/dimethenamid-P + saflufenacil	735 + 25 g ai/ha	Corn (*Zea mays* 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		
		Glyphosate + imazethapyr	900 + 100 g ai/ha	Corn- PP	Soltani et al. (2017)
		Prosulfuron + Bromoxynilb	10 + 140 g ai/ha	Winter wheat (*Triticum aestivum* L.) - POST	
		Glyphosate	1.68 kg ae/ha		Stachler and Kells (1997)
		Glyphosate +2,4-D ester	1.68 + 0.56 kg ae/ha	–	
		2,4-D amine	1.1 kg ae/ha	–	Stachler et al. (2000)
		Metribuzin + Chlorimuron	297 + 28 g ai/ha		
		Linuron + Chlorimuron	563 + 31 g ai/ha	Soybean (*Glycine* max (L.) Merr)- PRE	
		Chlorimuron	12 g ai/ha	Soybean- POST	
		MON 12000 + MON 13900 + Pendimethalin + Paraquat	84 + 252 + 1121 + 515 g ai/ha	Corn- PRE	
		Atrazine	2241 g ai/ha		
Post-Emergence		CGA-152005	30 g ai/ha	Corn- POST	Stachler and Kells (1997)
	Overwintered	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.

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 and Brunet, 2017). Furthermore, Stachler and 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). 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.

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.

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.

CRediT authorship contribution statement

Asharp Godwin: Writing – original draft, Visualization, Methodology, Investigation, Formal analysis, Conceptualization. **Simone Pierialli:** Writing – review & editing, Supervision, Methodology, Conceptualization. **Svetla Sofkova-Bobcheva:** Supervision, Methodology, Conceptualization. **Andrew Ward:** Supervision, Conceptualization. **Craig McGill:** Writing – review & editing, Supervision, Project administration, Methodology, Investigation, Funding acquisition, Conceptualization.

Declaration of competing interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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