

RESEARCH ARTICLE

Bioclimatic analysis of potential worldwide production of spring-type camelina [*Camelina sativa* (L.) Crantz] seeded in the spring

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Abstract

Camelina [*Camelina sativa* (L.) Crantz] is a Brassicaceae oilseed that is gaining interest worldwide as low-maintenance crop for diverse biobased applications. One of the most important factors determining its productivity is climate. We conducted a bioclimate analysis in order to analyze the relationship between climatic factors and the productivity of spring-type camelina seeded in the spring, and to identify regions of the world with potential for camelina in this scenario. Using the modelling tool CLIMEX, a bioclimatic model was developed for spring-seeded spring-type camelina to match distribution, reported seed yields and phenology records in North America. Distribution, yield, and phenology data from outside of North America were used as independent datasets for model validation and demonstrated that model projections agreed with published distribution records, reported spring-seeded camelina yields, and closely predicted crop phenology in Europe, South America, and Asia. Sensitivity analysis, used to quantify the response of camelina to changes in precipitation and temperature, indicated that crop performance was more sensitive to moisture than temperature index parameters, suggesting that the yield potential of spring-seeded camelina may be more strongly impacted by water-limited conditions than by high temperatures. Incremental climate scenarios also revealed that spring-seeded camelina production will exhibit yield shifts at the continental scale as temperature and precipitation deviate from current conditions. Yield data were compared with indices of climatic suitability to provide estimates of potential worldwide camelina productivity. This information was used to identify new areas where spring-seeded camelina could be grown and areas that may permit expanded production, including eastern Europe, China, eastern Russia, Australia and New Zealand. Our model is the first to have taken a systematic approach to determine suitable regions for potential worldwide production of spring-seeded camelina.

KEYWORDS

bioclimatic model, Brassicaceae, *Camelina sativa*, climate, CLIMEX, oilseed crop

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1 | INTRODUCTION

Camelina [*Camelina sativa* (L.) Crantz, Brassicaceae] is an ancient oilseed that is gaining interest as a low-maintenance crop in different regions of the world, such as Canada and the northern United States (Blackshaw et al., 2011; Scott et al., 2021), Europe (Zanetti et al., 2021), Russia (Kon'kova et al., 2021) and China (Gao et al., 2022). Its agronomic attributes, such as a short growing season (Plessers et al., 1962), shatter resistance (Zubr, 1997), resistance to common Brassica pests (Soroka et al., 2015) and diseases (Séguin-Swartz et al., 2009), tolerance to drought (Hunsaker et al., 2011) and low temperature (Putnam et al., 1993), good performance on light soils and relatively low input requirements (Ehrensing & Guy, 2008) make it an attractive alternative for farmers interested in diversifying their crop rotation, particularly on low-quality land where other oilseeds do not perform well. Camelina has a unique seed oil composition, characterized by a combination of high contents of unsaturated fatty acids (ca. 90%) and tocopherols and low levels of the undesirable fatty acid, erucic acid (<4%), rendering camelina oil well-suited for a wide variety of applications, ranging from food and feed to industry (Abramović et al., 2007; Righini et al., 2016; Vollmann & Eynck, 2015; Zubr, 1997; Zubr & Matthäus, 2002). In particular, camelina has been identified, together with other Brassicaceae species, like pennycress (*Thlaspi arvense* L.) and carinata (*Brassica carinata* L.) as a feasible option for sourcing a low indirect Land Use Change feedstock for sustainable aviation fuel (Taheripour et al., 2022). The global aviation sector currently almost entirely relies on fossil fuels and accounts for approximately 2% of global anthropogenic greenhouse gas (GHG) emissions (Cames et al., 2015). As the aviation industry pledges to halve emissions by 2050 relative to 2005 levels (ICAO, 2016) and renewable jet fuel produced from biomass is recognized as the most technically feasible means to reducing the GHG intensity of jet fuel (de Jong et al., 2018), interest in camelina as an industrial feedstock crop should further increase.

Camelina originated in the steppe regions of south-eastern Europe and southwestern Asia; however, it is well adapted to a wide range of environments (Knörzer, 1978; Zanetti et al., 2017; Zohary & Hopf, 2000). For a comprehensive review of its worldwide distribution, the reader is referred to Francis and Warwick (2009).

Climate is the dominant factor that determines the distribution and abundance of plants and animals (Andrewartha & Birch, 1954) and one of the most important factors influencing the productivity of crops (Hatfield et al., 2011, 2020; Zanetti et al., 2017). Some studies demonstrated that weather effects had a greater impact on camelina seed yield than genotype (Masella et al., 2014; Załuski

et al., 2020; Zanetti et al., 2021). Guy et al. (2014) stated that to further the ongoing effort of promoting camelina production, growers and the seed industry need to gain an understanding of the variability and adaptation potential of camelina across environments. Models can contribute to this understanding, as modelling crop response to climatic factors and weather is required for accurate prediction of crop response to impacts of climate and weather variability (Boote et al., 2013).

A few models have been developed to simulate meteorological and climate impacts on camelina. CAMEL, for example, is a model based on daily weather inputs that can be used to predict crop phenology, productivity and seed quality in northern Italy (Cappelli et al., 2019). CAMEL was extended to simulate fatty acid composition of the seed oil (Fila et al., 2020). Both models were developed for field scale analysis. Falasca et al. (2014) developed an agro-climatic zoning model to identify potential growing areas for camelina seeded in the spring in Argentina; the authors stated that the model could be applied to any part of the world, but no published worldwide predictions are available, to our knowledge. The development of a bioclimate model may be a useful method for analyzing the relationship between climatic factors and camelina yield and for identifying regions with potential for camelina production on a worldwide scale.

The bioclimatic modelling software CLIMEX, originally developed to simulate the distribution and abundance of arthropod pests, plant pathogens and weeds, has been successfully used for cultivated crops including tomato (*Solanum lycopersicum* L.), maize (*Zea mays* L.) and date palm (*Phoenix dactylifera* L.) (da Silva et al., 2018; Ramirez-Cabral et al., 2017; Shabani et al., 2012; Sutherst et al., 1996; Sutherst & Maywald, 1985). CLIMEX enables the development of models that describe the potential distribution and relative abundance of a species based on climate (Kriticos, Maywald, et al., 2015; Sutherst, 2000; Weiss et al., 2022). CLIMEX models allow researchers to gain an understanding of the climatic factors that affect species distribution and abundance and permit identification of non-climatic factors that limit species distribution (Sutherst & Maywald, 2005). Model parameters include temperature, photoperiod, moisture, heat stress, cold stress, wet stress, and dry stress. CLIMEX models infer a species' response to climate based on its geographic range, phenology, relative abundance, and empirical data. Model outputs include the ecoclimatic index (EI) that describes species-specific climatic suitability at various spatial levels. The growth index (GI) describes the potential for growth during the growing season and is the product of indices for temperature, moisture and photoperiod. EI values are derived by combining the GI

with stress indices and its values range from 0 (where the species is not able to persist) to 100 (where conditions are optimal for species survival) (Kriticos, Brunel, et al., 2015). EI values are set to 0 if the computed number of potential degree-days (PDD) is less than the PDD threshold value for a particular species.

The primary objective of this study was to develop a bioclimate model specifically for *spring-seeded spring-type camelina* (hereafter, simply camelina). Spring-type camelina is the most widely cultivated biotype of this species and efforts to scale up the commercial development of winter camelina are relatively recent (Berti et al., 2016). Using the validated model, the secondary objectives of the study were to: (1) conduct bioclimatic analyses (e.g., sensitivity analyses using incremental scenarios) to develop a better understanding of how climate affects spring-seeded camelina production and (2) identify new regions suitable for camelina production and regions where camelina is already grown that have potential for increased future production in a spring seeding scenario.

While spring-type camelina cultivars can be seeded in the fall in regions with mild winters (Berti et al., 2016), our model focuses solely on camelina seeded in the spring; the rationale being that compared to the large number of publications treating the spring-seeded crop (reviewed in for example Berti et al., 2016; Zanetti et al., 2021), there is a dearth of published scientific studies on fall-seeded spring-type camelina (Angelini et al., 2020; Berti et al., 2011; Masella et al., 2014; Righini et al., 2019; Royo-Esnal & Valencia-Gredilla, 2018). Consequently, data related to winter stress of spring-type camelina cultivars are insufficient for development of a model for fall-seeded spring-type camelina.

2 | MATERIALS AND METHODS

2.1 | Model development

The bio-climatic modeling process used herein has been previously described (Floate et al., 2017; Vera et al., 2002; Yonow et al., 2021). CLIMEX models derive EI values that describe the climatic suitability, in terms of species survival and reproduction, for specific regions. The calculation of an EI integrates the weekly response of a species to climate using a series of annual and weekly indices. An annual GI describes the potential for crop production as a function of precipitation, temperature and photoperiod during the growing season. Up to eight stress indices (cold, wet, hot, dry, cold-wet, cold-dry, hot-wet and hot-dry) are used to simulate factors that limit productivity during inclement conditions. The weekly growth index (GI_w) is a function of computed indices

for weekly temperature (TI_w), moisture (MI_w) and light (LI_w), which are comprised of limiting low and high values as well as optimal low and high values. Weekly stress indices include cold (CS), heat (HS), wet (WS) and dry (DS) stress and consist of threshold values and stress accumulation values based on linear rates. The growth and stress indices are calculated weekly and then combined into an overall annual index of ecoclimatic suitability (EI), which ranges from $EI = 0$ for locations at which the species is not able to persist to $EI = 100$ for locations that are optimal for species survival.

The CLIMEX model required five climatic inputs: temperature (maximum and minimum), precipitation, and relative humidity (at 09:00 and 15:00 h). Monthly climate data were used as an input for the Compare Locations function, a module that allows output of annual and weekly index values, including one EI-value for each grid cell (Kriticos et al., 2012). The dataset represents a splined 10' world grid data set that includes a hybrid data set (based on CRU CL2.0 and WorldClim, centered on 1975). The moisture index (MI) is based on a calculated soil moisture value. CLIMEX uses a hydrological sub-model to compute weekly soil moisture balance based on soil moisture from the previous week and current week values for precipitation and evapotranspiration. CLIMEX further uses a degree-day model (Baskerville & Emin, 1969), to compute a temperature index (TI). Annual datasets were generated for each run and were analysed at the continental scale.

Model parameterization for camelina using CLIMEX 4.1 (Kriticos, Maywald, et al., 2015) was developed by iteratively adjusting parameter values to produce mapped results that closely approximated observed distribution records for *C. sativa* in North America (Francis & Warwick, 2009; GBIF.org, 2021) as well as reported data for crop phenology and seed yield. Initial parameter values were based on published data that resulted from laboratory and field studies (Blackshaw et al., 2011; Gugel & Falk, 2006; Guy et al., 2014; Plessers et al., 1962; Russo et al., 2010; Zanetti et al., 2017; Zubr, 2003). Once the North American distribution was defined, based on a visual comparison of model output with observed distribution, EI values were compared to reported data for seed yield. Data related to agronomic performance were used to further refine parameter values so that the highest EI values occurred where camelina was reported to have the highest seed yields and lower EI values were reported for regions where camelina was reported to have lower seed yields.

2.2 | Model validation

The model was validated by comparing output to independent data that reported distributions, seasonal

phenology and seed yield. Three methods were used to validate the model. First, independent worldwide distribution datasets and published reports (5623 in total) were used to compare predicted to actual distribution of *C. sativa* in Europe, Asia, Australia, Africa and South America. Second, model output for phenology was compared to published reports for Europe (Krzyżaniak et al., 2019; Załuski et al., 2020; Zanetti et al., 2017). Third, site-specific model results were compared with yield results obtained from European field trials (Alberghini et al., 2022; Krzyżaniak et al., 2019; Zanetti et al., 2017).

2.3 | Weekly index values

Weekly output was analyzed at the regional scale to conduct analysis of GI_w , TI_w , MI_w and LI_w at spatial and temporal scales. Eight locations were selected to analyse weekly response of camelina to climatic variables: Aliartos, Greece (38.5°N, 23°E); Bologna, Italy (44.5°N, 11.5°E); Fort St. John, British Columbia, Canada (56.5°N, 121°W); Ketrzyn, Poland (54°N, 21.4°E); Saskatoon, Saskatchewan, Canada (52°N, 106.5°W); Swift Current, Saskatchewan, Canada (50°N, 107.5°W); Taber, Alberta, Canada (49.5°N, 112°W); and Wageningen, The Netherlands (52°N, 5.5°E). For each location, a geographic rectangle, 2° latitude by 2° longitude was used to delineate a geographic region around each location, resulting in 144 grid cells. Model output was averaged across the 144 grid cells for each region to estimate index values for each location.

2.4 | Sensitivity analysis

Two methods were used to conduct sensitivity analysis to quantify the response of *C. sativa* to changes in precipitation and temperature. The first method was based on the CLIMEX parameter sensitivity analysis function. Model runs were conducted for North America whereby each model parameter (listed in Table 1) was individually adjusted upward and downward. CLIMEX's default perturbation values were assigned to each model parameter. An average deviance function was used to produce a sensitivity value for each variable and associated perturbation values. The second method required the development of incremental scenarios (Olfert et al., 2018, 2019; Weiss et al., 2022) to reflect the possible range of temperature and precipitation values, based on current climate, that could be expected to occur in North America and Europe. Scenarios were selected based on potential variation of present climate. EI values, based

TABLE 1 Values for parameter settings for the CLIMEX model projecting spring-seeded *Camelina sativa* distribution and productivity.

Index	Parameter	Description	Value
CLIMEX growth parameters			
Temperature (°C)	DV0	Limiting low temperature	5
	DV1	Lower optimal temperature	16
	DV2	Upper optimal temperature	24
	DV3	Limiting high temperature	34
Moisture ^a	SM0	Limiting low soil moisture	0.125
	SM1	Lower optimal soil moisture	0.2
	SM2	Upper optimal soil moisture	1.0
	SM3	Limiting high soil moisture	1.4
Light (daylength, h)	LT1	Limiting low daylength	12.5
	LT0	Optimal daylength	16.5
CLIMEX stress parameters			
Heat stress (°C)	TTHS	Heat stress temperature threshold	34
	THHS	Heat stress temperature rate	0.05
Dry stress ^a	SMDS	Dry stress threshold	0.125
	HDS	Dry stress rate	-0.01
Wet stress ^a	SMWS	Wet stress threshold	1.4
	HWS	Wet stress rate	0.01
Degree-days per generation	PDD	Minimum degree days above DV0	1050

^aSoil moisture as a function of soil capacity, for example a value of 0.5 indicates soil moisture content is 50% of capacity.

on current climate, were compared to scenarios that differed by: (a) -1°C and $+1^{\circ}\text{C}$ from current temperatures (average maximum and minimum monthly temperature values); and (b) -40% , and $+40\%$ of current average total monthly precipitation. Two additional incremental scenarios altered temperature and precipitation values to represent cool/damp growing seasons (-1°C and $+40\%$ precipitation) and warm/dry growing seasons ($+1^{\circ}\text{C}$ and -40% precipitation).

2.5 | EI values and crop yields

Camelina yield data were obtained from published and unpublished results (Data S1). Where multiple year results were available for a specific location, site-specific average yields (kg/ha) were computed. Average EI values for each site were calculated using EI values from 144

locations within a geographic rectangle, 2° latitude by 2° longitude, around each site where yield data were available. Based on these data, average yields and EI values were computed on a country basis. Published crop seed yields were averaged by country and compared to corresponding EI values to assess fit between model output and observed yields. A logarithmic regression was utilized to fit the relationship between EI and yield.

3 | RESULTS AND DISCUSSION

3.1 | Model development

Distribution data for North America (Figure 1) indicate that camelina production ranges from Mexico (19.16°N, 98.98°W) to northern Canada (58.41°N, 116.12°W) (GBIF.org, 2021; Plessers et al., 1962). Camelina is well adapted to cool temperature, semi-arid zones and may be found at higher altitudes in warmer zones of the United States (Francis & Warwick, 2009). CLIMEX sets EI values

to 0 if observed PDD does not exceed the parameterized value, indicating that the growing season is not long enough or temperatures are insufficient to permit the crop to mature. A number of authors have reported temperature threshold and degree-day requirements for camelina (Blackshaw et al., 2011; Krzyżaniak et al., 2019; Zanetti et al., 2017, 2021). Lower development threshold values (DV0) in the literature range from −0.1 to 5°C (Allen et al., 2014; Gesch, 2014). PDD requirements (spring-seeded camelina) noted in the literature range from 933 to 1411 degree-days (base 5°C) (Gesch, 2014; Krzyżaniak et al., 2019; Zanetti et al., 2017, 2021). Using a base value of 4°C, degree-day requirements ranged from 1147 to 1388 degree-days (Alberghini et al., 2022). Model iterations, based on DV0 values between −1 and 7°C and PDD values between 1000 and 1350 were tested to obtain agreement between observed *C. sativa* distribution for North America and model output (Figure 1). Sensitivity to either the threshold temperature or total degree days tends to be greatest for locations that are at the northern extent of the potential range for a given species, in this case, for camelina

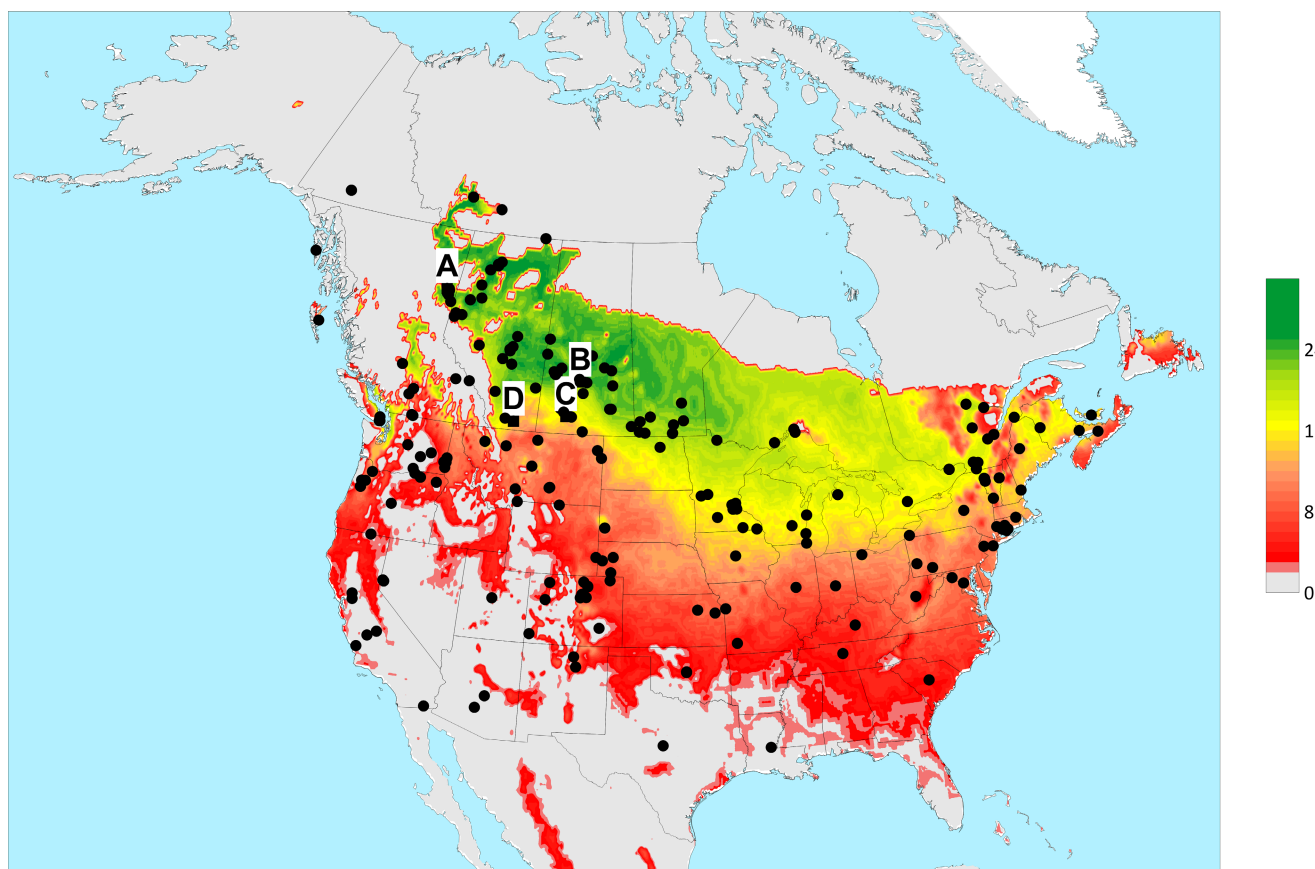


FIGURE 1 Distribution data, projected distribution and ecoclimatic index (EI) results for North America for (A) Fort St. John, British Columbia, Canada (56.5°N, 121°W); (B) Saskatoon, Saskatchewan, Canada (52°N, 106.5°W); (C) Swift Current, Saskatchewan, Canada (50°N, 107.5°W); and (D) Taber, Alberta, Canada (49.5°N, 112°W). Black symbols indicate distribution records obtained from GBIF (GBIF.org, 2021), CABI, GRIN and other published data sources. Ecoclimatic index values provide estimates of yield potentials across 30 year periods and large geographic ranges. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

production. Since field trials have been conducted at Fort Vermillion, Alberta (58.4° N, 116.12° W) and Fort St. John, British Columbia (56.5° N, 121.0° W) (Eynck et al., 2021; Plessers et al., 1962; Zanetti et al., 2017), the PDD value was parameterized to allow camelina production to occur in northern Alberta and British Columbia. Based on a DV0 value of 5°C, PDD values greater than 1100 resulted in camelina distributions that did not fully extend to the Peace River region of Canada, where camelina has been shown to perform well. Therefore, DV0 and PDD were set at 5°C and 1050, respectively (Table 1).

Parameterization of the lower (DV1) and upper (DV2) optimal threshold temperatures, based on published values, was not straightforward. DV1 was set to 16°C based on Russo et al. (2010) reporting that maximum germination of the camelina line NEB C-1 occurred at 16°C. Falasca et al. (2014) reported that temperatures of 10–22°C were suitable for reproductive development. DV1 and DV2 inputs are based on weekly temperatures required for optimum growth. For camelina, we propose that optimal growth is most critical during flowering and pod development. The majority of published values for seed yield were accompanied by average growing season temperatures (Gesch, 2014; Hossain, Johnson, Wang, Blackshaw, Cutforth, & Gan, 2019; Zanetti et al., 2017). Based on climate normals for June and July (Kriticos et al., 2012) and published yields, DV1 and DV2 were set to 16 and 24°C, respectively (Table 1). Oilseed crops that evolved in cooler climates may not be well adapted to warmer regions, such as southern USA. Thus, camelina seed germination was reported to decrease at temperatures greater than 30 and 32°C, respectively (Gesch, 2014; Russo et al., 2010). Parameterization of the upper temperature threshold (DV3) was set by conducting model runs between 30 and 40°C. Based on the distribution of camelina in southern USA, DV3 was set at 34°C (Table 1).

Soil moisture indices are defined by four parameters: lower soil moisture threshold (SM0), lower optimal soil moisture (SM1), upper optimal soil moisture (SM2) and the upper soil moisture threshold (SM3). Parameterization of limiting soil moisture (SM0) was based on values that may occur during germination and flowering and took into consideration that the permanent wilting point in CLIMEX is 0.1. Camelina germination was reported when soil moisture was as low as 5% (Končius & Karčauskienė, 2010). While CLIMEX model inputs are based on soil moisture, agronomic studies on camelina generally report seed yield potentials based on rainfall. Thus, parameter values were inferred, based on comparisons between climate rainfall values and published yield data. Based on conditions across the Canadian prairies and eastern Canada, SM0 was set to 0.125. Parameterization of lower (SM1) and upper optimal (SM2) values were set to 0.2 and 1.0, respectively.

A value of 0.2 was required for suitable growth across the southern Canadian prairies. The upper soil moisture threshold was set to 1.4 to allow for camelina production in wetter regions including eastern Canada (Table 1).

In North America, camelina occurs between 19.16° N and 61.87° N. Of 170 North American records, only nine were for latitudes less than 35.79° N (GBIF.org, 2021), suggesting that camelina crop potential may be responding to photoperiod and that the crop is adapted to longer day lengths (i.e., longer daily photoperiods). Limited production south of 36° N could be due to a number of factors, including photoperiod. The CLIMEX light index has two parameters, defining day lengths that prohibit growth (LT1) and the optimal day length (LT0). Based on distribution data, LT1 and LT0 were set to 12.5 and 16.5 h, respectively (Table 1).

CLIMEX models can account for abiotic stress indices (heat, cold, wet, dry, and interactions) to place limits on the potential range of a species due to unfavourable climate. No stress values for camelina have been reported in the literature, thus values were inferred from distribution data. Stress values were parameterized iteratively to define the modeled range of camelina in central and northern regions of North America to match its actual distribution. Heat stress is defined by two parameters: heat stress temperature threshold (TTHS) and heat stress accumulation rate (THHS). By definition, TTHS must be equal to or greater than DV3. Heat stress was parameterized to limit distribution for locations south of 36° N and the temperature threshold (TTHS) was set to 34°C and heat stress accumulation (THHS) was set at 0.05. The wet stress threshold (SMWS) was set to 1.4 with an accumulation rate (HWS) of 0.01. The dry stress threshold (SMDS) must be equal to or less than SM0; thus, SMDS was parameterized to 0.125 and the accumulation rate (HDS) was set to 0.05 (Table 1).

The resulting model was projected onto North America and compared with actual distribution data for camelina. Overall, the model projection agreed with distribution data (Figure 1). Greatest production, based on EI values, was predicted to occur across the American Midwest and the Canadian provinces of Ontario, Manitoba, Saskatchewan and Alberta. In this case, the model prediction agreed with numerous reports (Blackshaw et al., 2011; CFIA, 2017; Eynck et al., 2021; Gugel & Falk, 2006; Hossain, Johnson, Wang, Blackshaw, & Gan, 2019; Johnson, 2011; Malhi et al., 2014; Plessers et al., 1962). The model did not predict camelina production for locations in southern California, Nevada, southern Arizona and Washington (French et al., 2009; George et al., 2017; Lohaus et al., 2020; Pi et al., 2019) where camelina is grown with irrigation. Due to the worldwide objectives of this model, irrigation scenarios were not considered, but clearly, the global

distribution of camelina may be expanded to areas where irrigation is possible. The model indicated that there is very limited potential for camelina production in northern Texas, Arkansas, Mississippi, Alabama, Georgia, South Carolina and northern Florida. In a Texas field study comparing the yield potential of the oilseed crops rapeseed, flax, safflower and camelina at nine sites in a fall-seeding scenario, the seed yields of camelina were generally lower than those of the other species (Darapuneni et al., 2014). Likewise, a study to assess potential for large-scale camelina production for biofuel applications in Arkansas concluded that climate and terrain conditions in eastern Arkansas were not suitable (Tracy, 2017), corroborating the results of our model.

Comparison of crop development with model output is one method that can be used to assess fit of DVO and PDD. Model output was compared with growing season stages (seeding, flowering, harvest) to assess model output related to crop stage. The growing season was defined by the period where GI_w was greater than 0.1. Camelina field trials at Saskatoon, Saskatchewan (2015–2021) reported as average dates for seeding May 17, for flowering July 3 (two locations in 2020) and maturity July 31, resulting in 74 days from seeding to maturity (Eynck et al. unpublished data). The bioclimatic model indicated that seeding could occur during the latter half of April. Regardless of weather conditions on the Canadian prairies, oilseed seeding in experimental field trials in and around Saskatoon realistically does not occur until May. Predicted maturity dates were between July 19 and September 6; the average maturity date for Saskatoon was August 12. Model results indicated that maturity would occur in 87 days with an accumulation of 1071 degree days. At Swift Current, the average seeding date was May 10. Maturities were not recorded; the average harvest date was August 22. Assuming a maturity date of 10 days prior (based on results for Saskatoon), maturity was predicted to occur in 94 days with a degree day accumulation of 1046. The most northern field site was at Fort St. John, British Columbia, where the average dates for seeding were reported as May 18, for flowering as July 5 (range July 2–9) and for maturity as September 8 (range August 28–September 18). Model results indicated that seeding could occur in late April in the north, with first flowering on July 5 and maturity occurring on September 6. In the north, model predictions closely matched observed crop development. As such, the growing cycle at Fort St. John would take 2 weeks longer (111 days) than in Swift Current. Overall, model results closely agreed with observed results. Differences may be explained by the fact that model runs were based on climatic values, based on weekly results, not observed weather (daily) values.

3.2 | Model validation

3.2.1 | Distribution

Distribution data for Europe, Asia, Australia and South America were reserved for model validation. Modeled projections for *C. sativa* in these continents agreed with published reports (Brock et al., 2020; CABI, 2015; CFIA, 2017; Falasca et al., 2014; Francis & Warwick, 2009; GBIF.org, 2021; Krzyżaniak et al., 2019; Vollmann et al., 2007; Zanetti et al., 2017, 2021; Zubr, 2003). Camelina is well adapted to temperate climates and studies have shown that it has high yield potential in Central Europe (Krzyżaniak et al., 2019; Masella et al., 2014). The model projection agreed with the known European distribution and indicated that greatest crop production, based on EI values, would occur across eastern regions of central and northern Europe (Figure 2). Potential range and EI values agreed with reported camelina production across Scandinavia and western Russia (Kon'kova et al., 2021; Zubr, 2003). The model accurately predicted that camelina growth could occur across northern Europe (Peipohja, Finland; 61.26° N, 22.31° W) and western Russia (Pushkin, Russia; 59.71° N, 30.4° W) and confirms DVO and PDD values. The model predicted that EI values would be moderate across central Italy (Apennine Range); this is likely due to the moderating effect of altitude on climate. Model projections for Asia agreed with observed distribution where camelina is reported to occur across a number of countries extending from Georgia to Japan. The greatest number of observations occurred across most of southern Russia and eastern Uzbekistan; EI values were greatest across southern Russia (Figure 3a). Model results also agreed with published results for spring-seeded camelina across multiple locations in the semi-arid region of China (Gao et al., 2022; Zhang et al., 2021, 2022) and with camelina distribution in Australian and New Zealand (Figure 3b). A study conducted in southwestern Australia to assess production potential reported average yields of 1700 kg/ha (Francis & Campbell, 2003). However, the model predicted low EI values for western Australia, suggesting that growth potential for camelina in western Australia was very limited. The disparity between model EI values and reported yield (Francis & Campbell, 2003) could be because camelina in the study (which did not report seeding dates) was very likely seeded as a winter crop and the present model was developed for spring-seeded spring-type camelina.

The range of camelina in South America is limited to Chile and central regions of Argentina (GBIF.org, 2021); model output for South America closely matched the known distribution of camelina, but also indicated limited potential for camelina production in Uruguay and

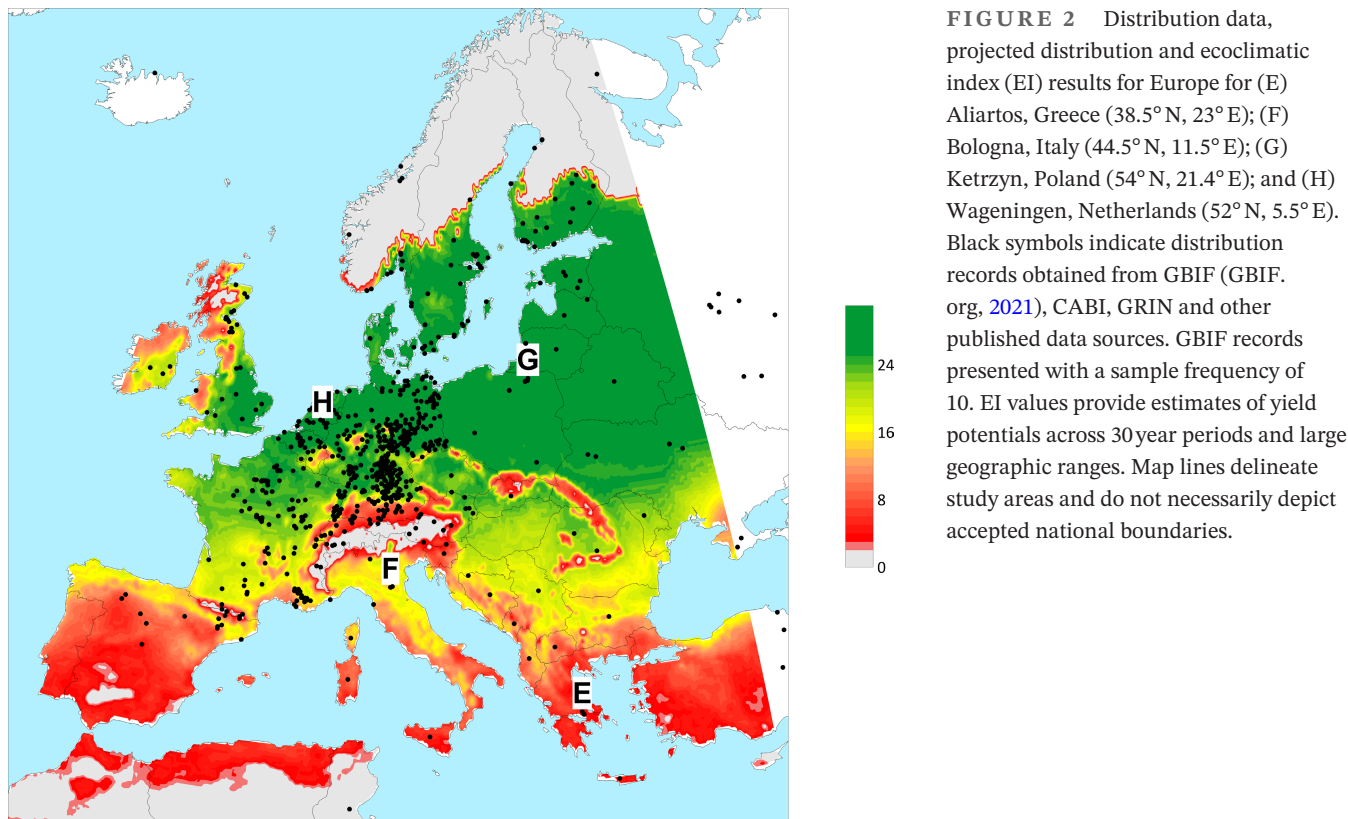


FIGURE 2 Distribution data, projected distribution and ecoclimatic index (EI) results for Europe for (E) Aliartos, Greece (38.5° N, 23° E); (F) Bologna, Italy (44.5° N, 11.5° E); (G) Ketrzyn, Poland (54° N, 21.4° E); and (H) Wageningen, Netherlands (52° N, 5.5° E). Black symbols indicate distribution records obtained from GBIF (GBIF.org, 2021), CABI, GRIN and other published data sources. GBIF records presented with a sample frequency of 10. EI values provide estimates of yield potentials across 30 year periods and large geographic ranges. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

southern Brazil (Figure 3c). Model results for Argentina indicated that optimal camelina production would occur across northern and central regions and was very similar to results reported by Falasca et al. (2014). Berti et al. (2011) conducted studies in Chile, with seeding dates ranging from April to August; therefore, mostly reflecting fall-seeded scenarios. Limited production potential is further predicted for parts of the Bolivian Andes, most likely again due to the moderating effect of altitude, similar to the situation for the Apennine Range in Central Italy. The model predicted low EI values (4–6) across northern Africa (Morocco, Algeria and Tunisia). Higher EI values (9–12) were projected for South Africa, southern Zimbabwe and a coastal region in southern Mozambique, in agreement with records of camelina production (without irrigation) in Africa (GBIF.org, 2021) (Figure 3d). Overall, predictions made by the camelina bioclimate model closely reflect records of observed distribution and production of spring-seeded camelina in non-irrigated fields; worldwide EI values are presented in Figure 4.

3.2.2 | Phenology

A valid bioclimate model must accurately predict growing season stages, in terms of spring-seeded crop flowering and crop maturity. Model output was compared with crop development for Lezany, Poland for the 2015–2018

growing seasons (Krzyżaniak et al., 2019). Model results for the Lezany region indicated that seeding should begin in early April, which agreed with seeding dates between April 7 and April 16 (Krzyżaniak et al., 2019). Model development was parameterized for optimal growth to occur during flowering and pod development. Based on $GI_w > 0.8$, our model predicted that flowering would begin in early June. Krzyżaniak et al. (2019) reported that flowering ranged from May 31 (2018) to June 10 (2015). GI_w declined during late July, indicating that camelina maturity was occurring and agreed with results from the Polish study. A 6-year study was conducted at Bologna, Italy (Alberghini et al., 2022; Zanetti et al., 2017). The average seeding date was March 18 (March 5–April 1) and was 18 days earlier than the model predicted. The average date of flowering was between May 17 and May 25 and was similar to the model prediction of mid-May. Maturity occurred from June 19 to July 3 (average was June 28) and was similar to the model prediction of maturity occurring in late June. Based on a study at Ketrzyn, Poland (Zanetti et al., 2017), seeding occurred April 14, 2015 and April 7, 2016 and was similar to model output that suggested that seeding could occur April 12. Maturity was predicted to occur in late July and agreed with reported maturity dates between July 30, 2015 and August 22, 2016. The seeding/maturity dates at Wageningen, The Netherlands were April 17, 2015 and July 31, 2015 (Zanetti et al., 2017) and were

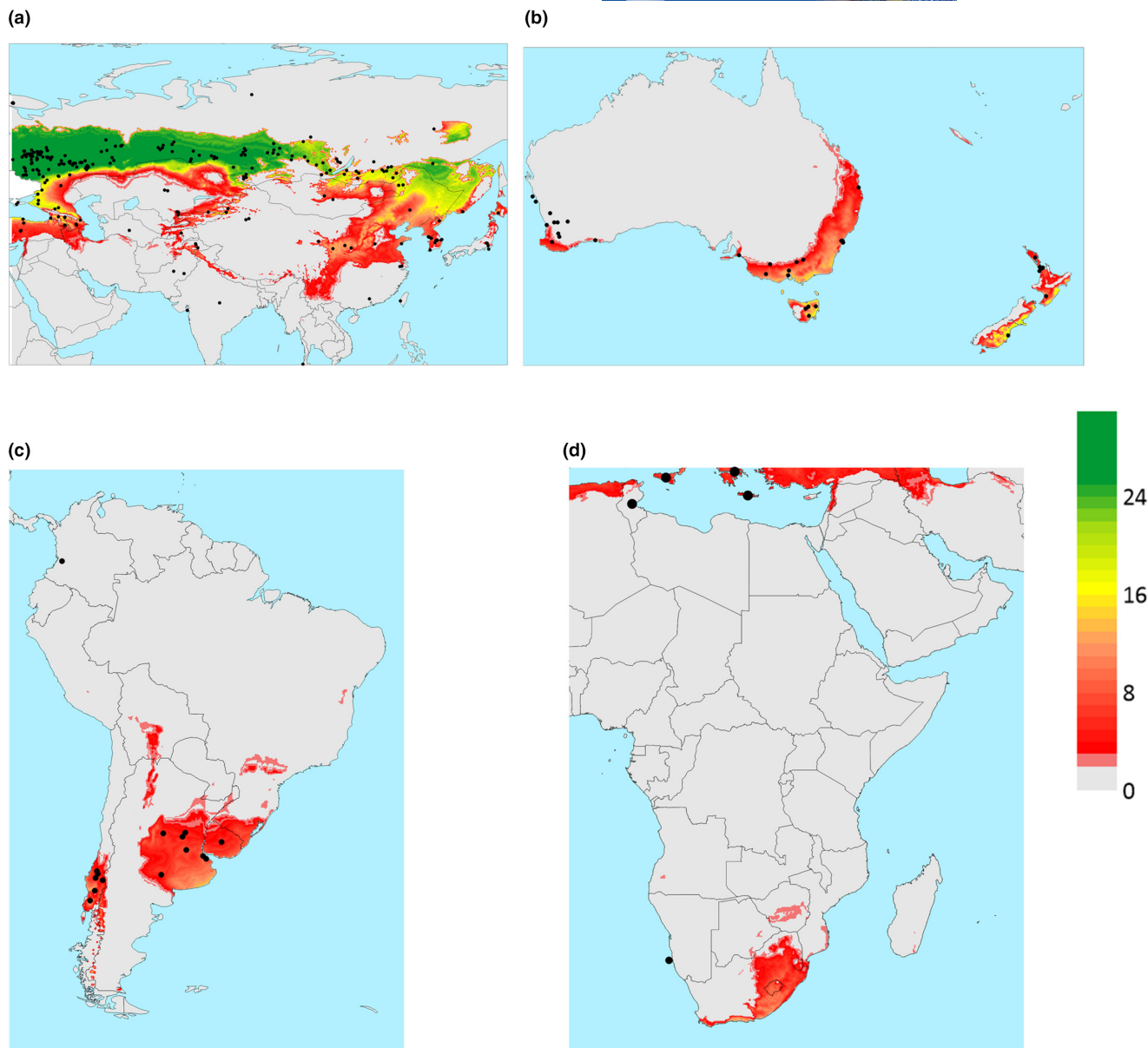


FIGURE 3 Distribution data, projected distribution and ecoclimatic index (EI) results for (a) Asia, (b) Australia, (c) South America and (d) Africa. Black symbols indicate distribution records obtained from GBIF (GBIF.org, 2021), CABI, GRIN and other published data sources. EI values provide estimates of yield potentials across 30 year periods and large geographic ranges. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

in close agreement with predicted values of April 12 and maturity beginning as early as July 19. Considering these studies report results across Europe, for specific dates, over short time intervals, relative to climate normal periods of 30 years, the results between field studies and model outputs are overall very similar.

3.2.3 | EI and crop yield comparison

Ecoclimatic index values provide an overall measure of the annual climatic suitability of a location for a particular

species. In the case of crops, such as camelina, the computed EI value represents a proportion of a year that is climatically suitable. Generally, camelina reaches maturity within 85–120 days after seeding; this represents a growth period that is between 25 and 33% of a year. Accordingly, the theoretical maximum EI value for a location that has a highly suitable climate for camelina production is also between 25 and 33, depending on spatial and temporal variation.

In order to validate EI values, model output was spatially compared with observed results for camelina productivity. Published crop seed yields were averaged

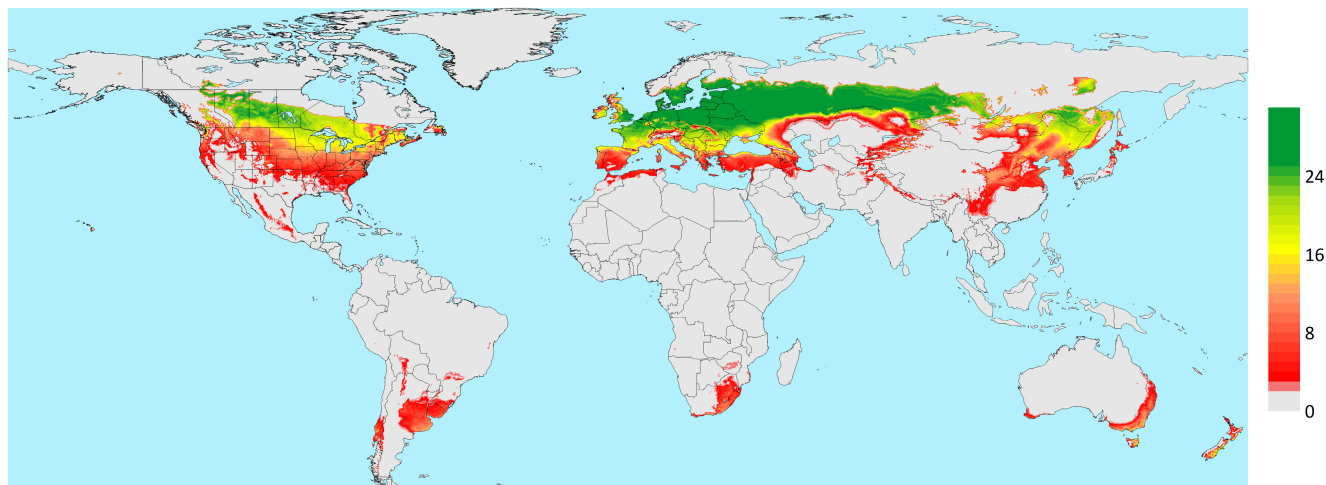


FIGURE 4 Projected worldwide distribution and ecoclimatic index (EI) for spring-seeded *Camelina sativa*. EI values provide estimates of yield potentials across 30 year periods and large geographic ranges. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

TABLE 2 Comparison of spring-seeded camelina yield (kg/ha) and EI values.

Country	Average yield	Average EI
Denmark	2600.0	26.7
Ireland	2400.0	16.7
Netherlands	2370.0	25.7
England	2343.0	21.3
Germany	2185.0	24.7
Canada	2111.6	19.2
Austria	2082.0	21.7
Poland	1917.5	27.0
Italy	1800.0	14.8
China	1705.5	8.6
Ukraine	1600.0	25.1
USA	1209.3	8.6
Chile ^a	575.5	6.3

Note: Based on data from Data S1, average yields and ecoclimatic index (EI) values were calculated for each country.

^aPresented yield data are for spring-seeded spring-type camelina (August seeding date, Date 5 in Berti et al., 2011).

by country and compared to corresponding EI values (Table 2; Figures 2 and 3) to assess fit between model output and observed yields. Trends for site-specific EI values were similar to those for yield results obtained from European field trials (Alberghini et al., 2022; Krzyżaniak et al., 2019; Zanetti et al., 2017). Thus, values were generally lowest for latitudes less than 47° N, including Spain, Italy, Greece and Turkey (Figure 2). The average EI value for Italy was 14.8 and the average yield was 1800 kg/ha. EI values were greatest across central

and northern Europe (greater than 51° N) and this corresponded to higher camelina yields. Yields greater than 2100 kg/ha were reported for Germany, England, The Netherlands, Ireland and Denmark (Agegenehu & Honermeier, 1997; Gehringer et al., 2006; Marquard & Kuhlmann, 1986; Pearson & Walker, 1999; Seehuber et al., 1987; Zanetti et al., 2017; Zubr, 1997). Based on EI value (16.7), the average seed yield reported for Ireland (2400 kg/ha) was greater than predicted (Crowley & Fröhlich, 1998). It should be noted that this value was based on a single study and may not reflect long-term average yields for Ireland. EI values for Ukraine (25.1) and Poland (27) predicted higher yields than observed (Czarnik et al., 2017; Gamayunova et al., 2019; Jankowski et al., 2019; Krzyżaniak et al., 2019; Zanetti et al., 2017). Differences may have been due to weather versus climate effects and/or agronomic factors.

For eastern Asia, the model output predicted that climatic suitability would be greatest in the northern region of China, including the provinces of Inner Mongolia and Heilongjiang, with EI values ranging from 12 to 24 (Figure 3a). EI values greater than 10 were predicted for a region north of 34° N and east of 101° E (Qinghai, Gansu, Shanxi, Henan, Qindao and Tongliao provinces). Reported seed yields for these regions ranged from 1081 to 2022 kg/ha (Gao et al., 2022; Zhang et al., 2021, 2022). EI values (5.6–6.9) for southern Chile (south of 35° S) indicated that yields in a spring seeding scenario should be very low (Figure 3b). Model output agreed with Berti et al. (2011) who reported yields of 514 and 637 kg/ha, respectively, for an August seeding date at the locations Gorbea and Osorno in southern Chile. Overall, EI values were in agreement with reported camelina seed yields for Europe, eastern Asia and South America.

3.3 | Weekly index values

Ecoclimatic index values summarize annual estimates of camelina response to climate. Growing season responses can be analysed with weekly output for GI_w , MI_w , TI_w , and LI_w (Figure 5). This type of approach is useful for providing a snapshot of the climatic conditions and their suitability during the growing season and for the comparative analysis of temporal responses for multiple locations. GI_w is a function of indices that are related to temperature, moisture, and photoperiod and was calculated for eight locations to analyze the response of camelina to climatic variables. While lower than at the other locations, weekly GI_w at Aliartos, Greece, is positive from late March to the end of June. At this location, GI_w is zero for July and August as a result of low TI_w , suggesting excessive temperature. MI_w values are at or near zero, indicating that moisture in the late summer months is generally insufficient (Figure 5a). In accordance with this, Zanetti et al. (2017) reported that irrigation had been applied during the 2015 and 2016 growing seasons. At Bologna, Italy, GI_w is positive from late March until mid-September. While moisture is sufficient for most of the growing season, temperature is a limiting factor during June and July (Figure 5b). Weekly indices curves are similar for Fort St. John, Canada, Ketrzyn, Poland, and Wageningen, The Netherlands (Figure 5c–e). At these locations, temperature and moisture are near optimal during late June and early July, resulting in GI_w values that were 0.9 or greater during the flowering period. Weekly indices curves were also similar for the three Canadian prairie locations, Saskatoon, Swift Current, and Taber (Figure 5f–h). Although MI_w was optimal, TI_w values decreased during the flowering period, indicating the potential for less than optimal conditions during flowering due to high temperatures (late June and early July). Lower MI_w values in July and August indicated sub-optimal moisture at these prairie locations during late summer.

3.4 | Sensitivity analysis

To assess the potential impact of each parameter on the model, sensitivity analyses were conducted using two methods. First, using the CLIMEX parameter sensitivity function, core distribution (CD) values were calculated to provide an estimate of where camelina production may be expected to occur with little or no stress (cold, heat, wet, dry stress) (Table 3). Sensitivity analysis indicated that CD was most sensitive to the dry stress threshold. Sensitivity to dry stress and heat stress thresholds indicated that the parameterization of lower moisture and upper temperatures are important factors to consider

during model development and that stress parameters related to drought have the greatest impact on the model. Sensitivity to all four moisture values (SM0, SM1, SM2, and SM3) was greater than to temperature variables (DV0, DV1, DV2, DV3). MI change was most sensitive to lower moisture thresholds (SM0 and SM1) and the TI sensitivity was greatest for the high limiting temperature (DV3), suggesting that regions that have excessively dry, warm growing seasons may not be conducive for camelina production. Although camelina is considered relatively drought tolerant, drought conditions, particularly during flowering, are known to have negative impacts on yield (Borzoo et al., 2020; French et al., 2009; Hunsaker et al., 1998, 2011). In terms of worldwide distribution, Range Change and EI were impacted by the threshold for degree days (1050 PDD) and the lower limiting temperature for development (DV0). These results reflect limits to the northward range extension of camelina.

Second, incremental climate scenarios were also conducted to determine how camelina range and EI (yield) respond to incremental variations in temperature and precipitation. Changes were compared relative to current climates for North America and Europe (Figures 1 and 2). In warmer than normal scenarios, EI values increased across the southern Canadian prairies while decreasing slightly across southwestern USA (Figure 6a). In cooler than normal growing seasons, EI values decreased, indicating a range contraction across northern Canada and a range extension across Texas and Oklahoma (Figure 6b). Guy et al. (2014) stated that camelina production in the US Pacific Northwest was at risk when precipitation was below normal. In concordance with this statement, the incremental scenario with 40% less precipitation reduced EI values, indicating a range contraction across western and central regions of North America (Figure 6c). In wetter growing season scenarios, EI values increased across most of western Canada but were lower in Minnesota (Figure 6d). In line with model predictions, it has been reported that excessive precipitation during spring was associated with lower yields (Gesch et al., 2015). A warmer (+1°C), drier (−40%) scenario provides insight to how camelina may respond to a growing season that would be similar to a drought (Figure 6e). This scenario resulted in a crop range response similar to the drier scenario (Figure 6c). Drought has been shown to reduce crop establishment, plant density, seed yield, quality, and to accelerate maturity (Gesch, 2014; Gugel & Falk, 2006; Leclère et al., 2021; Vollmann & Eynck, 2015). The cooler/wetter scenario results in changes to EI values similar to the cooler than normal scenario (Figure 6b).

Incremental scenarios were also analyzed for Europe, with similar trends as observed in North America. Warmer than normal conditions resulted in

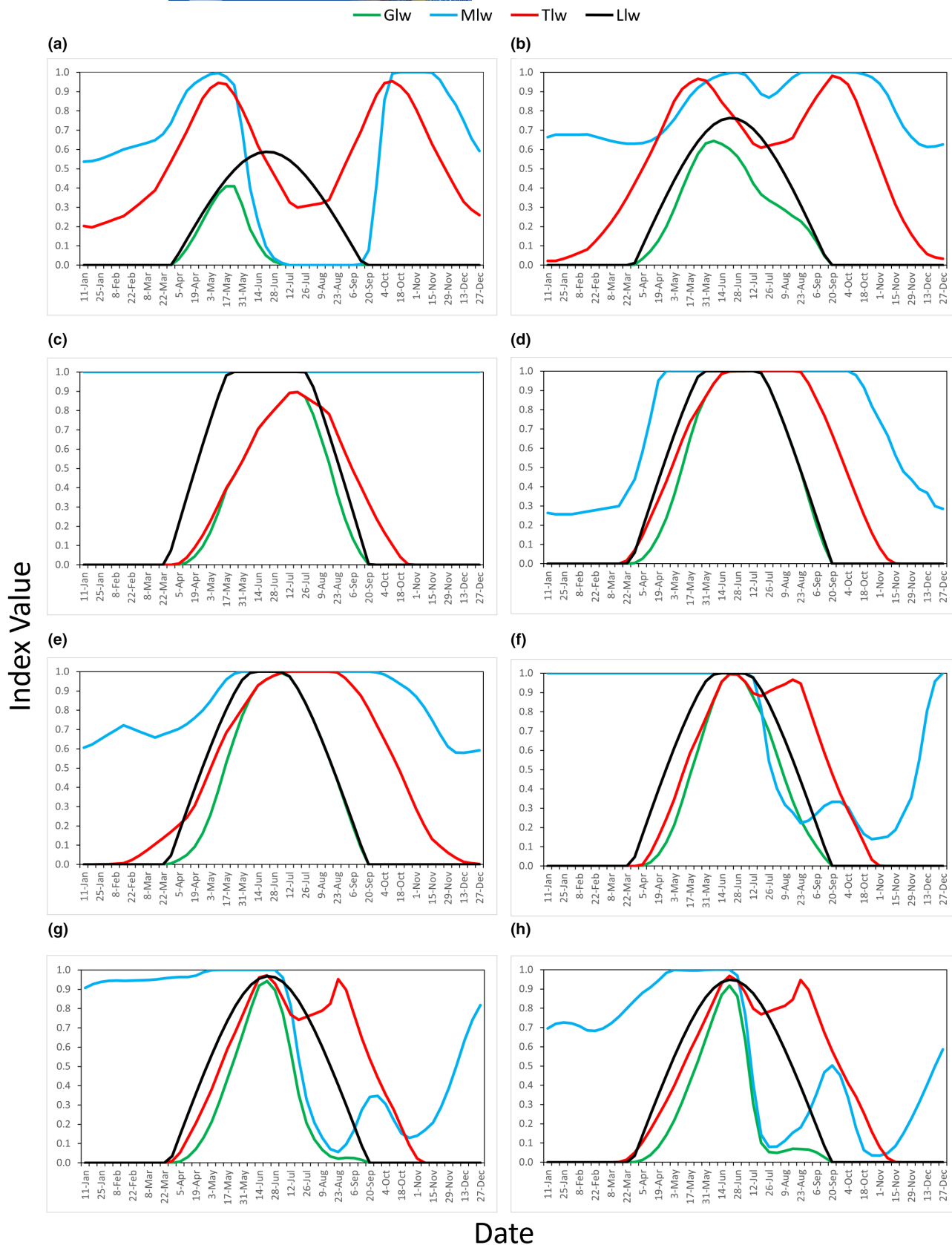


FIGURE 5 Weekly values for growth index (GI_w), moisture index (MI_w), temperature index (TI_w) and light index (LI_w) for (a) Aliartos, Greece; (b) Bologna, Italy; (c) Fort St. John, British Columbia, Canada; (d) Ketrzyn, Poland; (e) Wageningen, Netherlands; (f) Saskatoon, Saskatchewan, Canada; (g) Swift Current, Saskatchewan, Canada; (h) Taber, Alberta, Canada. Weekly values were obtained by calculating the average across all grid cells ($n = 144$) delineated by a geographic rectangle, 2° latitude by 2° longitude centered on each location.

TABLE 3 Sensitivity analysis results for spring-seeded *Camelina sativa* model.

Parameter	Parameter	Low	Default	High	Range change	CD change	EI change	GI change	TI change	MI change	DS change	HS change	WS change
Limiting low moisture	SM0	0.025	0.125	0.2	1.2	0	1.2	2.2	0	19.18	0	0	0
Lower optimal moisture	SM1	0.125	0.2	0.3	0.6	0	1.4	2.6	0	18.65	0	0	0
Upper optimal moisture	SM2	0.9	1	1.1	0.1	0	0.9	1.1	0	10.57	0	0	0
Limiting high moisture	SM3	1.3	1.4	1.5	0.3	0	0.8	1.2	0	9.01	0	0	0
Limiting low temperature	DV0	4	5	6	4.1	0	5.3	1.1	2.1	0	0	0	0
Lower optimal temperature	DV1	15	16	17	0	0	0.9	1.5	3	0	0	0	0
Upper optimal temperature	DV2	23	24	25	0.2	0	0.6	0.6	3.2	0	0	0	0
Limiting high temperature	DV3	33	34	35	0.5	0	0.5	0.5	3.8	0	0	0	0
Heat stress temperature threshold	TTHS	33	34	35	0.9	1.33	0.4	0	0	0	0	21.47	0
Heat stress temperature rate	THHS	0.04	0.05	0.06	0.1	0.01	0.1	0	0	0	0	2.51	0
Dry stress threshold	SMDS	0.025	0.125	0.2	0.9	16.57	0.9	0	0	0	38.51	0	0
Dry stress rate	HDS	-0.012	-0.01	-0.008	0.1	0.48	0.1	0	0	0	6.19	0	0
Wet stress threshold	SMWS	1.3	1.4	1.5	0.2	2.33	0.6	0	0	0	0	0	12.24
Wet stress rate	HWS	0.008	0.01	0.012	0	0.14	0.2	0	0	0	0	0	3.51
Degree-days per generation	PDD	840	1050	1260	5.5	0	5.9	0	0	0	0	0	0

Note: Results are listed in descending sensitivity across the modelled range for North America. Temperatures are listed in °C. Values describe the mean sum square change in the value of each index value for all locations that were included in the analysis.

Abbreviations: CD, core distribution; DS, dry stress; EI, ecoclimatic index; GI, population growth index; HS, heat stress; MI, moisture index; TI, temperature index; WS, wet stress.

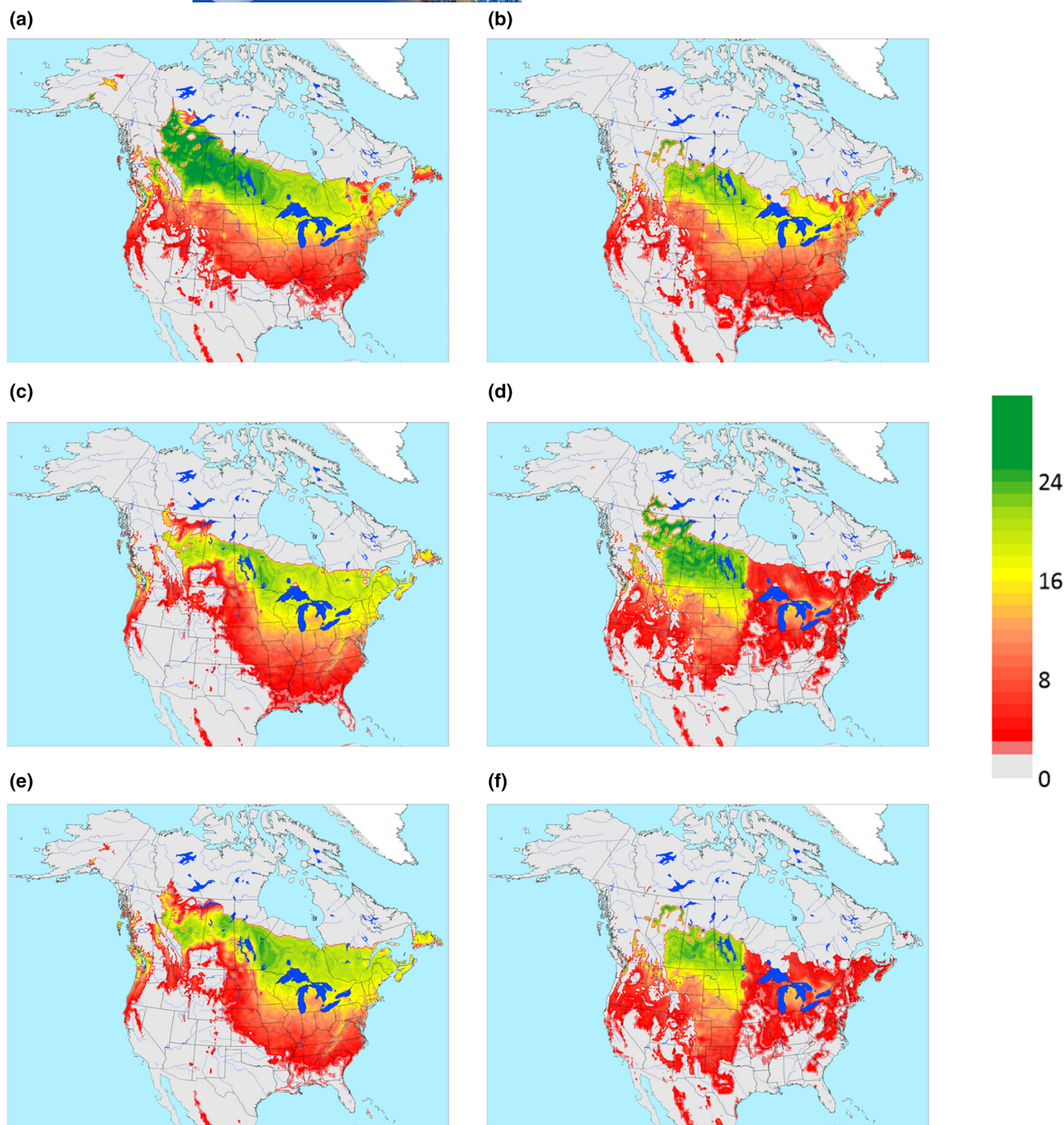
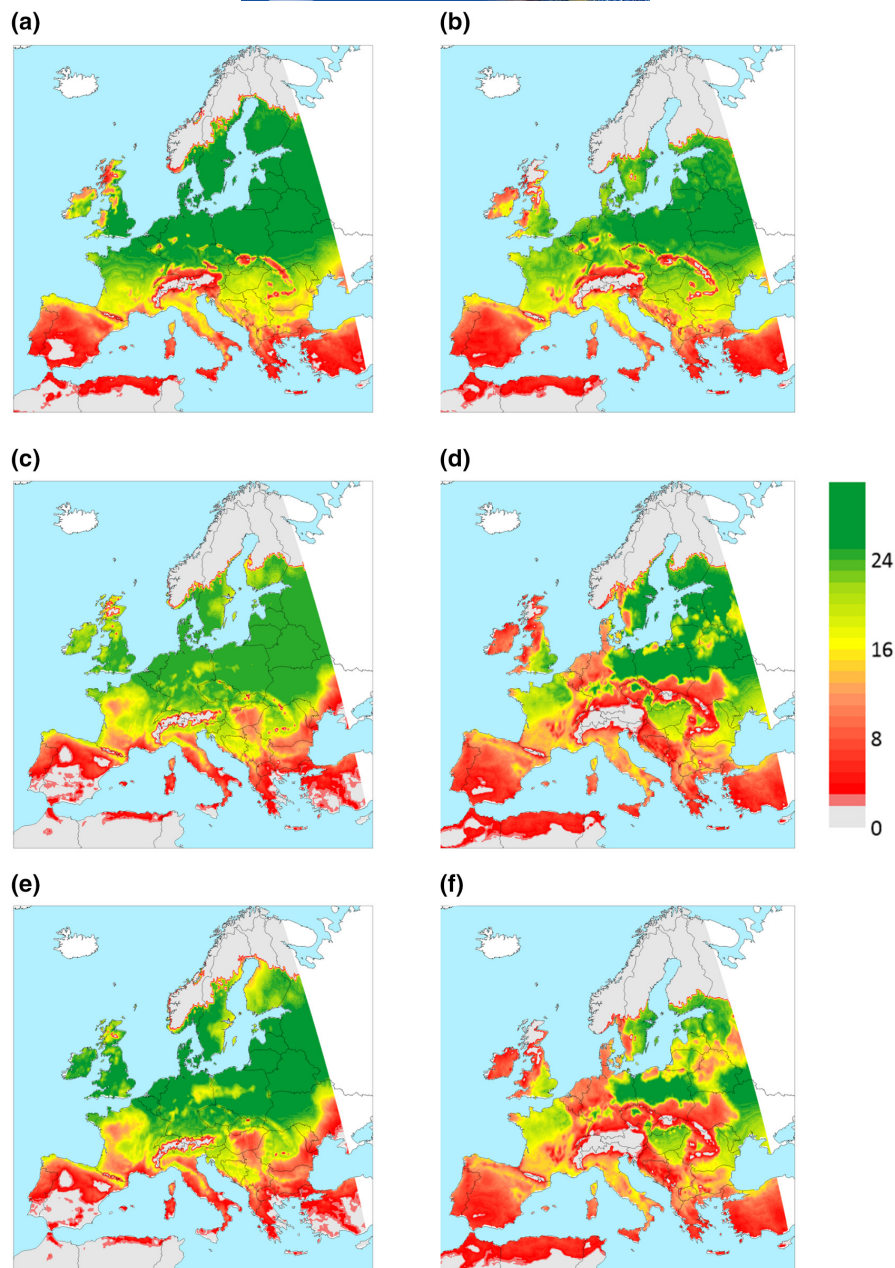


FIGURE 6 Predicted distribution and ecoclimatic-index values for spring-seeded *Camelina sativa* for North America with temperatures that are 1°C warmer (a) and 1°C cooler (b) than current climate; rainfall that is 40% less (c) and 40% greater (d) than current climate; climates that are 1°C warmer/40% drier (e) and 1°C cooler/40% wetter (f) than current climate. Map lines delineate study areas and do not necessarily depict accepted national boundaries.

predicted range extension across northern Europe and range contraction for Spain (Figure 7a), while a cooler growing season resulted in range contraction and EI reduction across northern Europe (Figure 7b). Reduced precipitation resulted in reduced range and EI or range (Figure 7c) for southern regions of Spain, Italy, Greece, and Turkey. A wetter growing season is predicted to

result in lower EI values across southern Germany, Austria, Hungary, and eastern Ukraine (Figure 7d). The drought scenario was predicted to have the greatest impact across southern Europe (Figure 7e). A cooler and wetter growing season is expected to result in reduced EI values and range contraction across central and northern Europe (Figure 7f).

FIGURE 7 Predicted ecoclimatic-index values for spring-seeded *Camelina sativa* for Europe with temperatures that are 1°C warmer (a) and 1°C cooler (b) than current climate; rainfall that is 40% less (c) and 40% greater (d) than current climate; climates that are 1°C warmer/40% drier (e) and 1°C cooler/40% wetter (f) than current climate. Map lines delineate study areas and do not necessarily depict accepted national boundaries.



3.5 | EI values and crop yields

Using camelina yield data obtained from published studies ($n=63$ sites), and our own as of yet unpublished research ($n=5$ locations) (Data S1), a regression analysis was used to establish if there is a relationship between EI values and yield. Yield can be predicted by EI values using $y=612.73\ln(x)+154.29$, where y =yield and x =EI value for a given location. The variability in EI values explains 27.9% ($R^2=0.2787$) of the variance in observed camelina yields. Similar yield/climate variabilities have been reported for maize, wheat (*Triticum aestivum* L.) and soybean (*Glycine max* L.) (Ray et al., 2015). Based on global averages, Ray et al. (2015) reported that 32%–39% of crop yield variability was explained by climate variability. Yield

estimates, as a function of climate, are further complicated by spatial and temporal scales (Liu et al., 2020). Climate is only one factor that contributes to crop yield. Other factors that are not incorporated into the bioclimate model include crop genetics, agronomic practices (seeding rate, planting date and fertilizer management), soil types, biotic stressors, and extreme weather events. Over the last decade, plant breeding efforts have resulted in improved camelina cultivars with increased seed size, seed yield, and yield stability (Alberghini et al., 2022; Eynck et al., 2021; Zanetti et al., 2017) and several studies have increased our understanding of how best to grow the crop (Berti et al., 2016; Gesch, 2014; Johnson, 2011; Malhi et al., 2014; Urbaniak et al., 2008a, 2008b). Zaluski et al. (2020) reported that environmental conditions, including weather,

explained 72.7% of camelina yield and daily meteorological data was used by Alberghini et al. (2022) to explain camelina yields. Differences in results between these studies and the current study can likely be explained by the fact that the studies by Załuski et al. (2020) and Alberghini et al. (2022) were based on meteorological data and not climate data. Meteorological values are based on daily values and are location-specific. Climate data, on the other hand, uses monthly mean values that are averaged over 30-year time periods. In this study values are presented as interpolated values. Thus, bioclimate models tend to produce conservative results that are useful at regional, national, or continental resolutions. In particular, yield results were obtained over shorter time periods and exhibited greater year to year variability while EI values provide estimates of yield potentials across 30-year periods and over large geographic ranges. The average yield of camelina was 1743 kg/ha (Data S1). Based on the relationship of EI and camelina yield, EI values can be used to summarize yield potential at regional scales (Table 4).

3.6 | Potential for camelina production

Several studies have been conducted to improve camelina productivity, often at regional scales. For example, Alberghini et al. (2022) conducted an analysis of growing seasons to identify growing conditions conducive for camelina production. Zanetti et al. (2013) identified potential European regions for camelina production based on a study of European environmental stratification (Metzger et al., 2005). Falasca et al. (2014) developed an agro-climatic model to assess potential regions in Argentina that may be suitable for camelina production in Argentina. In contrast, no studies have taken a systematic approach to determine suitable regions for potential worldwide production of camelina. An objective of this study was to use our bioclimatic model to identify new regions that are suitable for camelina production and

TABLE 4 Ecoclimatic index (EI) values, corresponding yields and yield potential categories for the spring-seeded *Camelina sativa* model.

EI	Yield (kg/ha)	Yield potential category
<2	<579	Minimal yield
2.1–6	580–1252	Well below average
6.1–10	1253–1565	Below average
10.1–18	1566–1925	Average
18.1–24	1926–2102	Above average
>24	>2103	Well above average

Note: EI and yield values were based on Data S1.

identify regions where camelina is grown that have potential for increased production on a worldwide scale, in a spring seeding scenario. The model results indicate potential for camelina production in large regions of north-eastern China (Heilongjiang, Inner Mongolia) and eastern Russia, where EI values are greater than 18 (Figure 3a). EI values for southeastern Australia (Victoria, New South Wales, and Tasmania) and New Zealand also indicate reasonable potential for camelina production (Figure 3b). The bioclimatic model may also be useful to identify regions that are expected to have higher yields than is currently observed. The model suggests, based on high EI values, that Eastern Europe has potential for higher than average camelina yields (Figure 2). However, yields in Eastern Europe are lower than in the Canadian prairies, even though EI values for the two regions are similar. Although the regions are climatically similar, agronomic factors, including seeding depth and stand establishment, soil types and biotic stressors, such as weed competition and disease, likely explain the discrepancy. Agronomic improvements and genetic improvements through breeding efforts may result in yields in eastern Europe that are more similar to those in the Canadian prairies. According to our model, expanded production may be possible in Poland, Lithuania, Latvia, Estonia, Belarus, and northern Ukraine.

4 | CONCLUSIONS AND MODEL LIMITATIONS

This study developed a model to conduct bioclimatic analysis of worldwide production of spring-seeded *C. sativa* and used the model to develop a better understanding of how climate may affect camelina production potential. The analysis resulted in the identification of areas that may permit expanded production (relative to current production, e.g., eastern Europe) and new areas where camelina could be grown (e.g., northeastern China). Results from the analyses predicted that spring-seeded camelina production will exhibit yield shifts at the continental scale as temperature and precipitation deviate from current conditions. A robust assessment of climate change impacts on camelina production in current growing regions and modelling the changes to determine optimal geographical ranges is a key component of planning and developing climate change adaptation strategies for this novel and promising crop in a variety of agroecosystems. The model developed here can be extended for the purposes of climate change analyses and can serve as a basis for the development of models for camelina in other production scenarios, such as spring-type camelina seeded in the fall or winter-type camelina. It is our hope that going forward, it may serve as a support tool for anybody with an

interest in identifying areas that are best suited for camelina production in one of the above-mentioned cropping scenarios. Furthermore, our work corroborates earlier studies that demonstrated that CLIMEX models can be successfully developed for a crop species. Thus, the model that was developed for camelina herein can be adapted to other, related crops that have similar climatic requirements.

One limitation of the bioclimate model is that the data available for model development were limited to existing distribution data for the species under study in the region used for model development and does not account for human intervention, which is an essential element contributing to the distribution of a crop or domesticated species. Fundamentally, without the introduction of *C. sativa* to New World countries by European settlers in the 19th century, camelina would most likely not exist in North America today. Similarly, there may be regions in the world that are conducive for camelina production that our model predicted to have limited potential. This disparity in model predictions and actual potential exists because the crop has not yet been introduced to these regions or other regions with similar climate and thus there are no distribution records to utilize in the modelling process. As such, there may be potential for camelina production in some areas in central Africa which are currently excluded from the model because the lower photoperiod threshold for the model was set to a 12.5 h photoperiod based on the current southern extent of camelina production in North America (i.e., no records south of 19.2° N in Mexico; GBIF.org, 2021; George et al., 2017). Similarly, the scarce distribution data for *C. sativa* in northern Canada (Yukon, Northwest Territories) determined that the lower PDD threshold be set to 1050, which resulted in the predicted range for camelina in Europe failing to encompass some of the current distribution data for Scandinavia. In this situation, model predictions for Europe were limited by the availability of distribution records in northern Canada, probably because camelina is a new and niche crop and because the infrastructure to handle camelina grain is not yet established. This hypothesis is supported by the observation that *Brassica rapa*, also known as Polish canola, a crop that has similar DVO and PDD requirements as camelina and a much longer history as a well-established crop, is widely distributed in northern Canada (GBIF.org, 2022). This scenario exemplifies the importance of the human element in the predicted and observed distribution range of camelina. Multi-year performance trials at several sites are needed in order to conclusively establish whether camelina is indeed a crop that is well-suited for production in the southern ranges of northern Canada and to parts of Africa. With new distribution data, arising from

efforts to establish the crop in new regions, the bioclimate model can be refined via re-parameterization and revalidation.

Last but not least, while the model presented herein focuses on spring-type camelina seeded in the spring (February–June in the Northern hemisphere; August–November in the Southern hemisphere), there are several regions in the world with mild winters that allow for fall (or winter) seeding of spring-type camelina (Berti et al., 2011; Masella et al., 2014). This is possible because even spring-type camelina plants are extremely frost tolerant in the seedling and rosette stage (Angelini et al., 1997; Putnam et al., 1993). However, as only a small number of scientific studies on fall-seeded spring-type camelina exist in the published literature (e.g., Angelini et al., 2020; Berti et al., 2011; Masella et al., 2014; Righini et al., 2019; Royo-Esnal & Valencia-Gredilla, 2018) as compared to the literature available for spring-seeded spring-type camelina, we opted to focus this CLIMEX model only on the spring-seeded scenario. As such, we recognize that the bioclimate model that we report here only pertains to the potential to grow spring-seeded spring-type camelina and does not account for the great potential of fall-seeded spring-type camelina that has been recorded in areas including California and the southern United States, Chile, Argentina, southern Brazil, and western Australia, or account for spring-type camelina potential in regions where the crop can be seeded in both the spring and the fall, such as in the Mediterranean (Righini et al., 2019). With the publication of additional studies on the production of fall-seeded spring-type camelina, it will become feasible (and necessary) to develop a CLIMEX bioclimate model specifically to account for the fall seeding scenario.

AUTHOR CONTRIBUTIONS

Ross M. Weiss: Conceptualization; data curation; formal analysis; investigation; methodology; visualization; writing – original draft; writing – review and editing. **Federica Zanetti:** Conceptualization; data curation; writing – review and editing. **Barbara Alberghini:** Data curation. **Debra Puttick:** Data curation; writing – review and editing. **Meghan A. Vankosky:** Writing – review and editing. **Andrea Monti:** Writing – review and editing. **Christina Eynck:** Conceptualization; data curation; formal analysis; investigation; visualization; writing – review and editing.

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CONFLICT OF INTEREST STATEMENT

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 STATEMENT

The data that support the findings of this study are openly available in “figshare” at <https://doi.org/10.6084/m9.figshare.24867417>.

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SUPPORTING INFORMATION

Additional supporting information can be found online in the Supporting Information section at the end of this article.

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