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Assessment of the suitability of Finnish climate for the establishment of *Fusarium circinatum* Nirenberg & O'Donnell



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Abstract

According to the EU plant health law, all Member States must carry out annual surveys for priority pests and emergency measure pests. However, surveys are not required for pests which, due to unsuitable ecoclimatic conditions, cannot become established in the considered Member State. This report presents our assessment of the suitability of the present Finnish climate for the establishment of *Fusarium circinatum*, the causal agent of pine pitch canker (PPC) and damping-off of pine seedlings, and which is regulated in the EU by emergency control measures.

We assessed the suitability of the Finnish climate for the establishment of *F. circinatum* outdoors by developing a global CLIMEX model for the potential range of PPC. Based on it, we assessed the likelihood of the Finnish climate for being suitable for the occurrence of PPC outdoors to be low, with a low level of uncertainty, and for the establishment of *F. circinatum* outdoors to be low, with a high level of uncertainty. In addition, based on a literature review, we assessed the likelihood of the temperature and moisture conditions in Finnish forest nurseries being suitable for the establishment of *F. circinatum* to be high, with a high level of uncertainty.

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EU:n kasvinterveysasetuksen mukaan kaikkien jäsenmaiden on vuosittain kartoitettava prioriteetti- ja hätätoimenpidetuhoojia. Kartoituksia ei kuitenkaan tarvitse tehdä tuhoojista, jotka eivät ilmastollisten olosuhteiden vuoksi pysty asettumaan kyseiseen jäsenvaltioon. Tämä raportti esittelee arviomme Suomen nykyisen ilmaston sopivuudesta pihkakoroa ja taimipoltetta aiheuttavan *Fusarium circinatum* -nimisen hätätoimenpidetuhoojan asettumiseen.

Arvioimme Suomen ilmaston sopivuutta *F. circinatum* -tuhoojalle pihkakoron esiintymistä ennustavan CLIMEX-mallin avulla, jonka kehitimme osana arviointityötä. Mallinnustulosten perusteella arvioimme todennäköisyyden, että Suomen ilmasto soveltuu pihkakoron esiintymiseen ja *F. circinatum* -tuhoojan asettumiseen, olevan pieni. Arvio ilmaston sopivuudesta pihkakoron esiintymiseen Suomessa on melko varma, kun taas arvio ilmaston sopivuudesta tuhoojan asettumiseen Suomeen on epävarma. Lisäksi arvioimme kirjallisuuskatsauksen perusteella todennäköisyyden, että suomalaisten metsätaimitarhojen lämpötila- ja kosteusolosuhteet sopivat *F. circinatum* -tuhoojan asettumiseen, olevan suuri. Arvio oli kuitenkin hyvin epävarma.

Beskrivning

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Enligt EU:s förordning om växtskydd måste alla medlemsländer årligen kartlägga skadegörare som är prioriterade och kräver nödåtgärder. Kartläggning behöver dock inte göras av skadegörare som på grund av klimatförhållandena inte kan etablera sig i den aktuella medlemsstaten. Denna rapport presenterar vår bedömning av förutsättningarna för det nuvarande klimatet i Finland för etablering av *Fusarium circinatum*, en skadegörare som kräver nödåtgärder eftersom den orsakar tallens hartskräfta och avdämpning.

Genom användning av CLIMEX-modellen som förutsäger förekomsten av tallens hartskräfta bedömde vi förutsättningarna med det finska klimatet för *F. circinatum*. Modellresultaten visade att sannolikheten för *F. circinatum* att orsaka tallens hartskräfta och etablera sig i det finska klimatet är låg. Bedömningen av lämpligheten av klimatet för tallens hartskräfta i Finland är relativt tillförlitlig medan bedömningen av förutsättningarna för etablering av skadegöraren i Finland är osäker. Dessutom bedömde vi, baserat på en litteraturöversikt, att sannolikheten för att temperatur- och fuktförhållandena i finska skogsplantager är lämpliga för etablering av *F. circinatum* är hög, men bedömningen är emellertid mycket osäker.

Contents

1	Backg	round and scope	7
2	An ove	rview of Fusarium circinatum	8
	2.1	The known global distribution of F. circinatum	8
	2.2	Host plants of F. circinatum	8
	2.3	Epidemiology of PPC outdoors	9
	2.4	Epidemiology of F. circinatum in forest nurseries	9
	2.5	Climatic requirements of PPC and F. circinatum	9
	2.6	Survival of F. circinatum without host plants	10
3	Suitab	ility of Finnish climate for PPC and the establishment of <i>F. circinatum</i>	
	outdo	Drs	11
	3.1	Developing and running a new CLIMEX model for PPC occurrence	11
	3.2	Suitability of the Finnish climate for PPC occurrence based on the	
		CLIMEX analysis	12
	3.3	Conclusion	13
4	Suitab	ility of temperature and moisture conditions for <i>F. circinatum</i> in	
	Finnish	n nurseries	14
	4.1	Conclusion	14
5	Refere	nces	16
Ar	nex I. D	evelopment of the global CLIMEX model for the potential range of PPC	20

1 Background and scope

The European Commission has established a list of 20 priority pests, whose economic, environmental, and social impact in the European Union (EU) is considered most severe (European Commission, 2019a). In addition, the Commission has active emergency measures for several pests.

According to the EU plant health regulation (European Union, 2016), all Member States must carry out annual surveys for each priority pest. Annual surveys are also required for many emergency measure pests. However, surveys are not required for pests for which it is unequivocally concluded that they cannot become established or spread in the Member State due to unsuitable ecoclimatic conditions or the absence of host plants.

For some of the priority and emergency measures pests, the likelihood of establishment in Finland or parts of Finland is currently highly uncertain due to potentially unsuitable ecoclimatic conditions. The Risk Assessment Unit of the Finnish Food Authority was requested to assess the suitability of the present Finnish climate for the establishment of these pests.

The assessments are mainly conducted based on non-systematic, yet thorough literature reviews. The literature search is conducted in the Web of Science (Clarivate Analytics, 2023), the European and Mediterranean Plant Protection Organization's (EPPO) Global Database (EPPO, 2023), and the European Food Safety Authority's (EFSA) publication database (EFSA, 2023), using the pest's name(s) and, if necessary, the name(s) of the disease(s) it causes as search words.

In some cases, the assessments may require modelling of the suitability of the climate for establishment. The potential need to model the suitability of the climate and the appropriate methods for modelling are evaluated based on the literature review.

By default, the assessments are made of the present Finnish climate, without considering the possible increase in climate suitability in the future Finnish climate due to global warming. **Factors other than the suitability of the climate are not considered in the assessment.**

The likelihood of the climate being suitable for establishment and the level of uncertainty of the assessment are rated with the following qualitative scales.

The likelihood of the climate being suitable for establishment	High	Moderate		Low
The level of uncertainty	High			Low

This report presents the assessment of the suitability of the present Finnish climate for the establishment of *Fusarium circinatum* Nirenberg & O'Donnell, the causal agent of pine pitch canker (PPC) and damping-off of pine seedlings, and which is regulated in the EU by emergency control measures (European Commission, 2019b).

2 An overview of Fusarium circinatum

Fusarium circinatum Nirenberg & O'Donnell (EPPO code: GIBBC) (synonym *Gibberella circinata* Nirenberg & O'Donnell) fungus is the causal agent of pine pitch canker (PPC) disease, which is a serious threat to pines (*Pinus* spp.) and Douglas fir (*Pseudotsuga menziesii*) globally (e.g. Wingfield et al., 2008). The pathogen can infect all parts of susceptible hosts of all ages (Wingfield et al., 2008), and in forest nurseries, it causes the pre- or post-emergence or late season damping-off of conifer seedlings (Viljoen et al., 1994; Gordon et al., 2001). In many cases, infection results in the death of host plant.

2.1 The known global distribution of F. circinatum

Fusarium circinatum is assumed to be native to Mexico, where PPC is widespread (Wikler & Gordon, 2000; Drenkhan et al., 2020). PPC also occurs in Colombia, Haiti, Japan, South Africa, South Korea, and the USA (in Alabama, Arkansas, California, Florida, Georgia, Indiana, Louisiana, Mississippi, North Carolina, South Carolina, Tennessee, Texas, and Virginia) (Drenkhan et al., 2020 and references therein). In Europe, PPC has been found in Spain (Landeras et al., 2005), Italy (Carlucci et al., 2007), Portugal (EPPO, 2019), and France (EPPO 2006). However, in Italy and France, the outbreaks have been successfully eradicated and nowadays *F. circinatum* is considered absent from these countries (EPPO, 2008; EPPO, 2023).

Fusarium circinatum occurs in forest nurseries in Brazil, Chile, Colombia, South Africa, and the USA (in Georgia and Indiana) (Drenkhan et al., 2020 and references therein). The pathogen has also been found in forest nurseries in Uruguay (Alonso & Bettucci, 2009), but the outbreaks have been successfully eradicated (EPPO, 2022). In Europe, *F. circinatum* has been found in forest nurseries in Spain (Landeras et al., 2005), Portugal (Braganca et al., 2009), and France (EPPO, 2009; EPPO, 2010).

2.2 Host plants of F. circinatum

Drenkhan et al. (2020) listed 138 known natural or artificial hosts of *F. circinatum*. Of these, 85 are species or hybrids in the genus *Pinus*. Natural infections have been recorded in 48 species or hybrids of the genus *Pinus* (Drenkhan et al., 2020). In non-pine tree hosts, natural infections have been recorded only in Douglas fir (*Pseudotsuga menziesii* (Mirb.) Franco) (Storer et al., 1994; Drenkhan et al., 2020).

The level of susceptibility to *F. circinatum* varies between host species, but also due to the age and provenance of the plants (Drenkhan et al., 2020). The susceptibility of Scots pine (*Pinus sylvestris* L.), which is the most common tree species in Finland, has been reported to vary from high to low (Enebak & Stanosz, 2003; Iturritxa et al., 2012; Iturritxa et al., 2013; Martínez-Álvarez et al., 2014; Martín-García et al. 2017; Davydenko et al., 2018; Martín-García et al., 2018; Woodward et al., 2022).

More recent studies have shown that *F. circinatum* can also colonise several grass species from Poaceae (Swett & Gordon, 2012; Swett et al., 2014; Swett & Gordon, 2015; Carter & Gordon, 2020; Herron et al., 2020) and dicots from Asteraceae, Convolvulaceae, Lamiaceae,

and Rosaceae (Hernandez-Escribano et al., 2018; Yang et al., 2019). Sporulation of *F. circinatum* on a grass host has been demonstrated in moist chamber experiments (Carter & Gordon, 2020), but the role of the non-coniferous hosts in the epidemiology of PPC or in the establishment of the pathogen is not yet known.

Nevertheless, these studies have prompted the hypothesis that grasses and dicots may actually be the primary resource for the fungus, and infections of pines have only occurred incidentally (Slinski et al., 2016; Gordon & Reynolds, 2017; Carter & Gordon, 2020; Carter & Gordon, 2021). This hypothesis is supported by findings that even a single selection round can significantly decrease the virulence of *F. circinatum* to pines (Slinski et al., 2016), and that there is a heritable variation in *F. circinatum* tolerance to grass defence compounds (Carter & Gordon, 2021).

2.3 Epidemiology of PPC outdoors

Typically, PPC occurs in mature trees, when *F. circinatum* has entered the host trees through wounds caused by insects, weather events, or silvicultural practices (Dwinell et al., 1985; Gordon et al., 2001). However, in some cases, mature trees may be infected even without wounds (Gordon & Reynolds, 2017; Swett et al., 2018).

The asexual spores (microconidia and macroconidia) of the pathogen are disseminated to new host trees by wind, insects, or water splash (Wingfield et al., 2008 and references therein). The conidial spores germinate in the wounds, and the pathogen subsequently penetrates the host tissue and eventually causes PPC in susceptible host plants (e.g., Wingfield et al., 2008). However, if the wounds become unsusceptible for the infection, e.g. dry out, before spore germination and the subsequent mycelial growth, the pathogen is unable to infect the host tree and cause the disease (Inman et al., 2008).

2.4 Epidemiology of F. circinatum in forest nurseries

Fusarium circinatum can enter forest nurseries via pine seeds, which it can colonise both internally and externally (Storer et al., 1998; Carey et al., 2005). After seed germination, the pathogen colonises the roots without necessarily causing any damage (Gordon & Reynolds, 2017). Swett et al. (2016) documented a symptomless biotrophic phase of *F. circinatum* in pine seedlings that persisted for at least one year. Moreover, this latent phase can even enhance the growth of the seedlings at first (Swett & Gordon, 2017), but when the pathogen eventually reaches the root collar, the damping-off symptoms typically start to develop (Swett et al., 2016).

2.5 Climatic requirements of PPC and F. circinatum

In mature trees, PPC occurs only in areas with relatively warm and moist climates (Gordon et al., 2001; Wingfield et al., 2008). For example, in California, occult precipitation such as fog or drizzle is considered the main reason PPC is more severe in coastal than inland areas (Wikler et al., 2003). However, moist periods that are too cool are thought to be the reason the disease is absent from the northern parts of California (Gordon et al., 2001; Inman et al., 2008; EFSA, 2010).

It has been suggested that in cool temperatures spore germination and the mycelial growth of *F. circinatum* is reduced, so that the wounds on the host trees become unsusceptible for the infection before the pathogen is able to penetrate the wounds and cause the disease (Inman et al., 2008). The occurrence of PPC in cooler areas is therefore generally considered very unlikely (Inman et al., 2008; Wingfield et al., 2008; EFSA, 2010). However, the climatic limitations may not apply if vector insects carry the pathogen deep into host tissues, where the required moisture for spore germination and mycelial growth is steadily available (Hoover et al., 1996; Gordon et al., 2001). This is particularly the case with the Monterey pine cone beetle (*Conophthorus radiatae* Hopkins; EPPO code: CONPRA), which is known to transmit *F. circinatum* to Monterey pines (*Pinus radiata* D. Don) in California (Hoover et al., 1996).

The optimal temperature for the spore germination of *F. circinatum* varies between strains, but in general, it appears to be 20–30 °C (Inman et al., 2008; Elvira-Recuenco et al., 2021). The optimal temperature for the mycelial growth of *F. circinatum* is around 25 °C (Inman et al., 2008; Mullett et al., 2017; Elvira-Recuenco et al., 2021), but this can also vary between the strains (Elvira-Recuenco et al., 2021). McDonald (1994) found no visible lesions on *Pinus radiata* at 10 °C, but Elvira-Recuenco et al. (2021) did find lesions at 10 °C, and they were about the same size as lesions at 20 °C.

2.6 Survival of F. circinatum without host plants

Fusarium circinatum is not known to produce any survival structures, but Elvira-Recuenco et al. (2021) observed hyphal melanisation of *F. circinatum* at 5 °C, which may have been related to the survival of the pathogen during harsh periods.

The pathogen can survive for at least six months in wet soil and one year in dry soil (Wingfield et al., 2008 referring to unpublished data by Gordon & Aegerter). Under controlled temperature and moisture conditions, conidia of F. circinatum have been recovered from soil with a moisture content of about 25% after 224 days at 5 °C and 20 °C, but not at 30 °C (Serrano et al., 2017).

The conidia may also survive in needle litter, but not at high levels (Aegerter & Gordon, 2006; Serrano et al., 2017). The pathogen has been recovered from infected wood debris after one year (McNee et al., 2002; Serrano et al., 2017) and from one infected branch even after three years (McNee et al., 2002).

3 Suitability of Finnish climate for PPC occurrence and the establishment of *F. circinatum* outdoors

Previously, the potential establishment of *F. circinatum* has been linked to the suitability of the climate for PPC occurrence (EFSA, 2010). This assumption is supported by the fact that the pathogen has been found outdoors only in areas where it causes PPC (Drenkhan et al., 2020). However, the findings of *F. circinatum* colonising non-conifers (see chapter 2.2) may indicate that the distribution of the pathogen does not entirely reflect the occurrence of PPC. Nevertheless, as there is currently no evidence that the pathogen could establish in non-coniferous hosts in a climate that is unsuitable for PPC, we used the suitability of the climate for PPC as a proxy for the suitability of the Finnish climate for the establishment of *F. circinatum* outdoors.

Various modelling frameworks have been developed to estimate the potential range of PPC based on climate suitability (Ganley et al., 2009; Watt et al., 2009; EFSA, 2010; Serra-Varela et al., 2017). Ganley et al. (2009) produced the first global estimate of the potential range of PPC using the bioclimatic modelling tool CLIMEX (Kriticos et al., 2015) and three-decade average climate data centred on 1975. Based on their results, the climate in Finland and other northern European countries is undoubtedly unsuitable for PPC occurrence.

The European Food Safety Authority (EFSA) assessed the suitability of the present climate in the EU for the establishment of *F. circinatum* based on the CLIMEX model by Ganley et al. (2009) but using a higher resolution and more recent climate data (1999–2007) (EFSA, 2010). Also based on this assessment, the climate in Finland and other northern European countries is unsuitable for the pathogen. EFSA (2010) concluded that the potential range of *F. circinatum* in the EU is limited by cold stress at high altitudes and latitudes and by dry conditions in other parts of the Union.

Recently, Drenkhan et al. (2020) confirmed the presence of PPC in several areas in South Korea, Mexico, and Spain, where the climate is considered unsuitable for PPC according to the CLIMEX analysis by Ganley et al. (2009). Furthermore, recent studies by Mullett et al. (2017) and Elvira-Recuenco et al. (2021) provide data on the influence of temperature on the hyphal growth and the lesion development of *F. circinatum* that somewhat conflicts with the data that were used to fit the CLIMEX model by Ganley et al. (2009). To obtain an up-to-date assessment of the suitability of the present Finnish climate for PPC occurrence, we therefore updated the global CLIMEX model for PPC occurrence by Ganley et al. (2009) based on the new observation records of PPC and the results of the recent phenological studies.

3.1 Developing and running a new CLIMEX model for PPC occurrence

We updated the global CLIMEX model for PPC occurrence by Ganley et al. (2009), using the Compare Location mode of the CLIMEX software, version 4.0.2 (Kriticos et al., 2015). The process of updating the CLIMEX model is presented in Annex 1.

To assess the suitability of the present Finnish climate for PPC occurrence, we ran the new CLIMEX model for Europe by using the climatological data on the present climate (three-decade average centred on 1995) in a 30-arc minute spatial resolution (Kriticos et al., 2012).

We used the same classification for the Ecoclimatic Index (EI), the index that defines climatic suitability, as Ganley et al. (2009), i.e. 0 = not suitable, 1–5 = marginally suitable, 6–20 = suitable and > 20 optimal.

To estimate the uncertainty of the new CLIMEX model results, we ran an uncertainty analysis using the Parametric Model Uncertainty algorithm in CLIMEX software, in which the parameter values are randomly sampled from probability distributions using a Latin hypercube sampling technique (Kriticos et al., 2015). The confidence limits, i.e. the minimum and maximum of the parameter values are defined by the CLIMEX software, and they are presented in Annex 1. The analysis was run using triangular distributions for the parameter values with 200 iterations. From the results, we explored the proportion of iterations in which the climate is considered optimal, suitable or marginally suitable for PPC occurrence (El > 0).

3.2 Suitability of the Finnish climate for PPC occurrence based on the CLIMEX analysis

The results of the new CLIMEX model are very similar to the results of Ganley et al. (2009) and EFSA (2010) and therefore suggest that the present Finnish climate throughout the country is unsuitable for PPC occurrence (Figure 1). The uncertainty analysis suggested the Finnish climate was not even marginally suitable for PPC occurrence in any of the runs (Figure 2).



Figure 1. The suitability of the European climate for PPC occurrence according to the new CLIMEX model developed in this study.



Figure 2. The uncertainty of the new CLIMEX model developed in this study. The results show the proportion of iterations in which the climate is considered optimal, suitable or marginally suitable for PPC occurrence (El > 0).

3.3 Conclusion

We rated the likelihood of the Finnish climate being suitable for the occurrence of PPC outdoors low, with a low level of uncertainty, and for the establishment of *F. circinatum* outdoors low, with a high level of uncertainty. The latter uncertainty is rated high because the pathogen may colonise many non-conifers, and it is unknown whether it could form viable populations on these hosts in a climate that is unsuitable for PPC occurrence.

While we rated the likelihood of the Finnish climate being suitable for the occurrence of PPC low, with a low level of uncertainty, it should be noted that some insects may be able to carry the pathogen deep into host tissues, where the climatic requirements for disease development are less critical. Since in the literature this concern has been related only to one insect species, whose importance as a PPC vector in the nature is still largely unknown, it didn't affect our conclusions.

It should be also noted that besides the climate, many other factors that are not considered in this assessment, such as the distribution of vector insects, susceptible host plants, natural enemies, and competitors, also affect PPC occurrence and the establishment potential of the pathogen. In particular, vector insects may have a huge impact on the occurrence of PPC as in some previous outbreaks there has been a clear association between insects and the disease occurrence.

4 Suitability of temperature and moisture conditions for *F. circinatum* in Finnish nurseries

The epidemiology and the environmental requirements of damping-off caused by *F. circinatum* forest nurseries differ from the epidemiology and the requirements of PPC (see chapters 2.3, 2.4, and 2.5). We therefore considered it necessary to separately assess the suitability of the temperature and moisture conditions in Finnish forest nurseries for the establishment of *F. circinatum*.

In Finland, the growth of coniferous forest seedlings starts in the spring in heated greenhouses, where the containerised seedlings are kept for two to three months before they are transferred outdoors. In most nurseries, the containerised seedlings are moved to winter storage containers in the late autumn. This provides stable temperature and moisture conditions for the seedlings during the winter. Damping-off caused by *Fusarium*, and other soil- or seed-borne fungal and oomycote species is a common problem in Finnish forest nurseries (Poteri, 2008; Lilja et al., 2010). From the genus *Fusarium*, at least *F. oxysporum* Schlechtendal (EPPO code: FUSAOX) and *F. avenaceum* (Corda) Saccardo (EPPO code: GIBBAV) are known to occur in the Finnish forest nursery production (Hanioja, 1969; Lilja et al., 1995).

Fusarium circinatum has thus far been found in forest nurseries only in areas where the climate outdoors is suitable for PPC occurrence (Ganley, et al., 2009; Drenkhan et al., 2020). However, several experts suggest that *F. circinatum* may also become a serious threat to forest nursery production in areas where the climate outdoors is unsuitable for PPC occurrence (EFSA, 2010; Gordon et al., 2015; Drenkhan et al., 2020). According to EFSA (2010), the same conditions in soil that enable the root growth of seedlings in nurseries enable damping-off infections by *F. circinatum*. According to Gordon et al. (2015), weather has only a minor effect on the activity of *F. circinatum* in soil. Drenkhan et al. (2020) argues that the stable temperature and moisture conditions typically maintained in nurseries are more suitable for disease development than the variable conditions outdoors. Despite these arguments, it appears that very little actual research has been done into the climatic requirements of *F. circinatum* in nurseries.

4.1 Conclusion

We rated the likelihood of the temperature and moisture conditions in Finnish forest nurseries being suitable for the establishment of *F. circinatum* high, with a high level of uncertainty. We rated the likelihood high because we assume that the temperature and moisture requirements of *F. circinatum* in forest nurseries do not significantly differ from the requirements of the *Fusarium* pathogens already occurring in Finnish forest nursery production. However, we rated the level of uncertainty high because it is not truly known whether the temperature and moisture conditions prevailing in forest nursery production in Finland and the climatic conditions when the seedlings are placed outdoors are suitable for the establishment of *F. circinatum*. Furthermore, there is thus far no evidence that the pathogen could establish in nurseries in areas where the climate outdoors is unsuitable for PPC occurrence.

It should be noted that besides temperature and moisture, many other factors, which are not considered in this assessment, such as the use of containerised seedlings, the preventive silvicultural treatments, and the survival potential of the pathogen without its host plants, presumably have a decisive effect on the establishment potential of the pathogen in Finnish forest nursery production.

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Annex 1. Development of the global CLIMEX model for the potential range of PPC

We developed a global CLIMEX model for the potential range of PPC occurrence (Figure 1) by updating the previous CLIMEX model by Ganley et al. (2009). The update was deemed necessary because PPC has recently been recorded in several locations in South Korea, Mexico, and Spain (Drenkhan et al., 2020) where the climate was considered unsuitable for PPC by the previous model (Ganley et al., 2009) (Figures 2, 3 and 4). In addition, recent studies by Mullett et al. (2017) and Elvira-Recuenco et al. (2021) have provided new information about the influence of temperature and moisture on the hyphal growth and lesion development of *F. circinatum*, which should be considered when fitting a CLIMEX model for PPC occurrence.

We developed the new CLIMEX model by using the Compare Location mode of CLIMEX software version 4.0.2 (Kriticos et al., 2015). We followed the main principles of CLIMEX when developing the model, i.e. we iteratively fitted the potential range of PPC occurrence to the known distribution records of the disease, but using parameter values that are reasonable and consistent with the known biology of the pathogen (Kriticos et al., 2015).

For the analysis, we used data on the present climate (three-decade average centred on 1995) in a 30-arc minute spatial resolution (Kriticos et al., 2012). We used the same classification for the Ecoclimatic Index (EI), the index that defines climatic suitability, as Ganley et al. (2009), i.e., 0 = not suitable, 1–5 = marginally suitable, 6–20 = suitable, and > 20 optimal.

Fitting the new CLIMEX model

Ganley et al. (2009) used CLIMEX parameters in various stress indices and degree-days required to complete the life cycle to constrain the potential range of PPC to the known distribution of the disease. When iteratively fitting the potential range of PPC, we found that the CLIMEX parameters for cold stress accumulation (THCS), high temperature thresholds (DV2, DV3, TTHW and TTHD), and degree-days required to complete the life cycle (PDD) limited the climate suitability for PPC within the new observation records of PPC in South Korea, Mexico, and Spain respectively.

The optimal temperature for the mycelial growth of *F. circinatum* is around 25 °C (Inman et al., 2008; Mullett et al., 2017; Elvira-Recuenco et al., 2021), but according to Mullett et al. (2017) and Elvira-Recuenco et al. (2021), growth is not significantly lower at 20 °C nor at 30 °C. According to Mullett et al. (2017), mycelial growth still occurs at 35 °C, but no longer at 40 °C. Hence, the upper optimal temperature value of 24 °C (DV2) and upper threshold temperature value of 31 °C (DV3) in the CLIMEX model by Ganley et al. (2009) (Table 1) appear to slightly underestimate the growth potential of the pathogen in high temperatures.

Consequently, we updated the CLIMEX model by Ganley et al. (2009) by redefining the parameter values of the cold stress accumulation rate (THCS), the upper optimal temperature (DV2), the limiting high temperature (DV3), the hot-wet stress temperature threshold (TTHW), the hot-dry stress temperature threshold (TTHD), and the degree-days

necessary to complete the life cycle (PDD) (Table 1). Overall, the new CLIMEX model indicates a lower accumulation of cold stress, better heat tolerance, and fewer degree-days needed for the disease development than the CLIMEX model by Ganley et al. (2009).

Table 1. The CLIMEX parameters and their values in the CLIMEX model by Ganley et al. (2009) and in the new CLIMEX model developed in this study. The parameter values that differ between the two models are in bold. The min and max parameter values of the new CLIMEX model were used to estimate the uncertainty of the new CLIMEX model results.

			This Study	
Parameter	Ganley et al. 2009	Estimate	Min	Мах
DVO-Lower temperature threshold	10	10	8	12
DVI-Lower optimal temperature	18	18	16	20
DV2-Upper optimal temperature	24	28	26	30
DV3-Upper temperature threshold	31	36	34	38
PDD-Effective accumulated temperature	1,150	1,000	800	1,200
TTCS-Cold stress temperature threshold	1	1	-1	3
THCS-Cold stress accumulation rate	-0.001	-0.0002	-0.00024	-0.00016
SMWS-Wet stress threshold	2	2	1.8	2.2
DTCS-Cold stress degree-day threshold	15	15	13	17
DHCS-Cold stress degree-day rate	-0.00027	-0.00027	-0.000324	-0.000216
HWS-Wet stress accumulation rate	0.002	0.002	0.0016	0.0024
SMO-Lower soil moisture threshold	0.3	0.3	0.1	0.5
SMI-Lower optimal soil moisture	1	1	0.8	1.2
SM2-Upper optimal soil moisture	1.5	1.5	1.3	1.7
SM3-Upper soil moisture threshold	2	2	1.8	2.2
SMDS-Dry stress threshold	0.3	0.3	0.1	0.5
HDS-Dry stress accumulation rate	-0.005	-0.005	-0.006	-0.004
TTHW-Hot-wet stress temperature threshold	30	36	34	38
MTHW-Hot-wet stress moisture threshold	1.4	1.4	1.2	1.6
PHW-Hot-wet stress accumulation rate	0.003	0.003	0.0024	0.0036
TTHD-Hot-dry stress temperature threshold	29	35	33	37
MTHD-Hot-dry stress moisture threshold	0.3	0.3	0.1	0.5
PHD-Hot-dry stress accumulation rate	0.05	0.05	0.04	0.06

Exploring the credibility of the new CLIMEX model

The new model predicts the climate to be more suitable for PPC occurrence in areas with recent new observations (South Korea, Mexico, and Spain) than the model by Ganley et al. (2009) (Figures 2, 3, and 4). The few remaining discrepancies between the results of the new model and observation records of PPC in northern Spain and Mexico may be due to model deficiencies or shortcomings in the climate data. The low 30-arc minute resolution climate data do not necessary capture the potentially huge variation in the local climates within a single grid cell. Consequently, some cells may be modelled as unsuitable for PPC occurrence, while certain local conditions within these cells could still be suitable for disease occurrence. Using the 10-arc minute resolution climate data would reduce this problem, but this climate data available for CLIMEX software is not up to date (three-decade average centred on 1975).

The new CLIMEX model predicts the climate to be suitable for PPC occurrence in some regions in the USA where the disease is absent (Figure 5). Again, this discrepancy may be due to model deficiencies, but it may also be due to the particular adaption of the local populations of *F. circinatum*. Indeed, the large variation in temperatures and precipitation within the known range of PPC could indicate that the pathogen has the potential to adapt to various climates (Drenkhan et al., 2020). This assumption is supported by the recent findings by Elvira-Recuenco et al. (2021) that the optimal temperature for spore germination, mycelial growth and lesion development varies between the strains of *F. circinatum*. Considering this scenario, the new CLIMEX model reflects the potential range of PPC covering all the known ecological variation in the climate adaptation of the pathogen, and therefore overestimates the potential range for a single local strain. This potential scenario should be considered if the model is applied in further studies or assessments.



Figure 1. The suitability of the climate for PPC occurrence based on the results of the CLIMEX model developed in this study.



Figure 2. The suitability of the climate for PPC occurrence in South Korea based on the results of a) the CLIMEX model developed in this study, b) the CLIMEX model by Ganley et al. (2009). The blue dots show the observations record of PPC uploaded from the Phytoportal geo-database (<u>http://bit.do/phytoportal</u>) developed by Drenkhan et al. (2020).



Figure 3. The suitability of the climate for PPC in Mexico based on the results of a) the CLIMEX model developed in this study, b) the CLIMEX model by Ganley et al. (2009). The blue dots show the observations record of PPC uploaded from the Phytoportal geo-database (<u>http://bit.do/phytoportal</u>) developed by Drenkhan et al. (2020).



Finnish Food Authority Research Resports 3/2023 | Assessment of the suitability of Finnish climate for the establishment of *Fusarium circinatum* Nirenberg & O'Donnell

Figure 4. The suitability of the climate for PPC in northern Spain based on the results of a) the CLIMEX model developed in this study, b) the CLIMEX model by Ganley et al. (2009). Figure 4 c) shows the survey locations of F. circinatum in northern Spain in the Phytoportal geo-database (<u>http://bit.do/phytoportal</u>) developed by Drenkhan et al. (2020). Not all the coordinates of the PPC records from Spain are available in the portal, and therefore we could not add the PPC records to figures 4 a) and b).



Figure 5. The suitability of the climate for PPC in the USA based on the results of the CLIMEX model developed in this study. The blue dots show the observations record of PPC uploaded from the Phytoportal geodatabase (<u>http://bit.do/phytoportal</u>) developed by Drenkhan et al. (2020).



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