



Climate change impact predictions on *Pinus patula* and *Pinus tecunumanii* populations in Mexico and Central America

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ABSTRACT

Climate change is likely to have a negative impact on natural populations of *Pinus patula* and *Pinus tecunumanii*, two globally important tree species in plantation forestry. The objective of this work was to evaluate the impact of climate change on the persistence of the natural populations of these species at their actual locations in order to take appropriate conservation measurements. A common approach to assess the impact of climate change on species natural distributions is climate envelope modeling (CEM). CEMs suggest significant impacts of climate change on the natural distribution of the two pine species, but their predictions contain considerable uncertainty related to the adaptive ability of tree populations to withstand future climate conditions. We assessed the adaptive ability of the two pine species based on the evaluations of provenance trials and used the results of these field trials to validate CEM impact assessment studies on provenance collection sites in the wild. The two pine species performed well in a wide range of climates, including conditions that were recorded by CEM as unsuitable for natural pine occurrence. The climate conditions where the two pine species naturally occur are predicted to become in the future more similar to the present climate of some areas where they are successfully established in field trials. These findings suggest that these pine species are in their natural habitat better adapted to climate change than CEM predicts. For the most vulnerable species, *P. tecunumanii*, human disturbances such as fragmentation from urbanization and conversion to agriculture that are occurring today are more urgent threats requiring action compared to the threat from climate change.

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1. Introduction

The scientific basis of climate change is now well established. Climate change has occurred in the past century and is likely to continue into the future (IPCC, 2007). Changing climate will most probably affect the geographic range of native trees and the locations where they can be grown in plantations as exotic species. The possible negative impacts on natural populations of important tree species should concern the forestry sector, as these are the source of genetic diversity (seeds) used to sustain and improve plantation productivity under both present and future conditions (Dvorak et al., 2008). Despite the importance of alterations in global temperature and precipitation patterns, considerable uncertainty still exists on how tree species will respond to changes in climate (Hamrick, 2004; Botkin et al., 2007; Kremer, 2007). It is

therefore important and relevant to better understand the threats of climate change to natural populations of tree species.

Many studies have used climate envelope models (CEMs) to assess the potential impact on ecosystems from climate change by using their current geographic distribution to develop a model of most suitable climate conditions for natural species occurrence, and projecting this into the future on the basis of results from general circulation models (GCMs). Their predictions show significant impacts and shifts in the actual distribution of many tree species (e.g. Gómez-Mendoza and Arriaga, 2007; Leng et al., 2008; Iverson et al., 2008). The extent to which trees can withstand environmental changes at their actual locations remains understudied in CEM-based climate change impact studies (Thuiller et al., 2007).

Although CEM modeling techniques have proved to be a valuable tool in the prediction of natural species distribution and the impact of climate change on their abundance (Guisan and Thuiller, 2005; Dormann, 2007), they face serious restrictions (Thuiller et al., 2004, 2007; Araújo et al., 2005; Dormann, 2007). One major problem with these approaches when applied to climate change research is that validation is difficult as the results

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are future projections (Araújo and Rahbek, 2006). Dormann (2007) highlights this as one of the top priorities for improving CEM predictions. Some authors use “hindcasting” to validate their models, whereby the past is used as a key to the future (e.g. Graham et al., 2004; Araújo et al., 2005). Another less used but potentially powerful approach is to couple the modeling with results from field evaluations where species survival and performance are measured under different climate conditions in so-called translocational experiments, including observations of trees planted outside their natural climate range as exotics (Zavaleta, 2006) or on sites where already moderate levels of climate change are observed (Thuiller et al., 2007).

It can be expected that the ability of tree species to persist at their actual locations under new climate conditions is key to their survival in the face of climate change. With the help of translocational experiments their adaptability to these new climate conditions can be quantified. In comparison to other plant life forms like herbs, ferns and mosses, trees are limited in their ability to shift to new areas of suitable climate due to their long growth cycle (Hamrick, 2004; Lenoir et al., 2008). Fragmentation due to human activities such as agriculture and urbanization further limits colonization of new areas that have potentially suitable climate (Davis and Shaw, 2001; Pearson and Dawson, 2003). Even if human disturbance is neglected, migration capacity of many tree species, especially those that are long-lived and form climax forest communities, might be too slow to keep pace with the predicted rapid changes in climate (e.g. Malcolm et al., 2002; McLachlan et al., 2005).

Provenance trials can be used to perform translocational experiments. Such experiments have been used in several studies to learn the niche breadth of tree species natural populations and niche variation between populations (e.g. Rehfeldt et al., 2002; Sáenz-Romero et al., 2006). Provenance trials are often established across a wider range of climate conditions than found in natural stands to determine the limits of their adaptability in new environments. Retrospectively they can be used to better climatic limits of populations in the wild.

Provenance trials exist for a number of economically important temperate and tropical tree species. For example, seed collections of 40 tropical and subtropical species in natural stands have been carried out by Camcore, North Carolina State University (International Tree Conservation and Domestication Program) for the last 3 decades and more than 1000 ha of field trials have been established (Dvorak et al., 2001). Results from these large scale field trials offer a unique dataset for better understanding the impacts of climate change on natural populations of the species, through a combination of climate envelope modeling and translocational validation based on provenance survival and growth.

This study aims to evaluate the performance of a climate envelope model for predicting climate change impacts by 2050 on natural populations of two important Mexican and Central American pines, *Pinus patula* and *Pinus tecunumanii* using results from provenance trials in Brazil, Colombia and South Africa as a means of validation. *P. patula* is native to eastern and southern Mexico (Perry, 1991) and *P. tecunumanii* is found predominantly in Central America and Chiapas, Mexico (Dvorak and Donahue, 1992). Nearly one million hectares of *P. patula* have been established in plantations, primarily in southern Africa (Birks and Barnes, 1991). Lesser amounts of *P. tecunumanii* are used in plantations, but it is an important plantation species in Colombia, and is gaining in importance in Brazil and South Africa (Dvorak et al., 2000a). Numerous provenance trials of *P. patula* and *P. tecunumanii* have been established by Camcore members in different tropical and subtropical regions. The specific objectives of this paper are to evaluate potential impact by 2050 of climate change on the wild distribution of the two species, to validate future predictions of

species distribution based on translocational trial data and to define the conservation implications of the findings for the two species under study.

2. Materials and methods

For each pine species, suitable areas for natural species occurrence were predicted under present climate and the expected climate in 2050 using the CEM modeling program “Maxent” developed by Phillips et al. (2006). We identified trial sites that had a present climate close to the present and predicted future climate of provenance locations in the wild, and used field evaluations from those trial sites as an independent source for validation of the CEM predictions on natural pine distribution. The adaptive ability of both pine species was assessed based on the natural climate ranges and the climate ranges in which the two species successfully were established in field trials.

2.1. Location data

We derived coordinates of 24 provenance locations in the wild of *P. patula* and 41 provenance locations of *P. tecunumanii* from seed collections provided by Camcore (Hodge and Dvorak, 1999; Dvorak et al., 2000b). The data set of *P. patula* provenance collection sites was complemented with a further seven points from the herbarium of Missouri Botanical Garden (Tropicos.org., 2008), providing a total of 31 geo-referenced locations representing natural populations of *P. patula*. Coordinates of all locations were checked following Hijmans et al. (1999) and are considered to be correct.

2.2. Study area

The study area was defined for each pine species based on the geographic range of the provenance collection sites. For the predictions of natural species occurrence and climate change impact, these areas were limited with a buffer of 3° from the most eastern, western, northern and southern provenance collection sites. The largest group of populations of *P. patula* occurs in the Sierra Madre Oriental in the eastern part of Mexico between 18°N and 24°N latitude, while outlier populations occur in the southern Mexican states Guerrero and Oaxaca between 16°N and 17°N latitude (Dvorak et al., 2000b). Natural stands are normally found in cloud forests at altitudes of 2100–2800 m (Perry, 1991). Natural stands of *P. tecunumanii* are found from Chiapas, Mexico (17°N) to central Nicaragua (12°N) (Dvorak and Donahue, 1992). *P. tecunumanii* distribution can be divided into two sub-population groups based on altitude of the collection sites: high elevation populations that are commonly found in cloud forests between altitudes of 1500–2900 m, and low elevation populations that occur between altitudes of 450 and 1500 m (Dvorak et al., 1989).

The climate change impact predictions from CEM on natural occurrence of the two pine species were validated based on height and survival data from eight-year-old established provenance trials planted in Colombia, Brazil and South Africa by Camcore members between 1982 and 1996 (Hodge and Dvorak, 1999; Dvorak et al., 2000a,b). In order of the 3 countries, data of *P. patula* provenances came from 8, 11 and 9 trial locations and of *P. tecunumanii* provenances from 11, 7 and 17 trial locations. Trial management (site preparation, spacing of trees, weed control, etc.) among studies was as similar as practical in the field.

2.3. Climate variable selection

CEM predictions become more biased by climate variables when they are extrapolated to areas outside the study area where

they were calibrated (Phillips et al., 2006; Randin et al., 2006). This happens also when applied into the future under climate change projections as climate moves beyond the bounds of the original calibration and in some areas enters into globally novel climates (Williams et al., 2007). These challenges occur in our study, and therefore we aimed to select only the most characteristic climate variables for use in the modeling, capturing those most significant in defining the natural species range, which also reduces model redundancy.

The 19 Bioclim variables (Busby, 1991), derived from the WorldClim database developed by Hijmans et al. (2005) were chosen to describe the climate in our study area. The WorldClim surfaces had a resolution of 5 km. Since climate variables are often highly correlated (e.g. Dormann, 2007), we first aimed to minimize redundancy by selecting single variables that are representative of other variables. To achieve this, correlating climate variables were clustered following the SAS VARCLUS procedure (SAS, 2003). In this multivariate technique, the clusters are chosen to maximize the variation at the first component of each cluster, and can be used to reduce the number of variables (SAS, 2003).

We then did a second filter of variable selection by using random distributions and Mann–Whitney *U*-tests. 500 random locations in a buffer of 300 km around the provenance collection sites were generated in ArcView 3.2. We then compared the climate of the provenance locations with the climate conditions of the random points, and the variables with the greatest differences from the Mann–Whitney *U*-tests were considered to be of most importance in defining the species range, as the species are not distributed randomly in their natural distribution.

To define the final variable set for the analysis, we selected from each cluster the climate variable that varied most significantly from the Mann–Whitney *U*-test (Table 1). The selected variables were considered to be representative of the other variables in the clusters, and were used in all further analyses. Some clusters did not contain any variables that distinguished significantly provenance locations from surrounding areas, so no variables from those clusters were included. Climate values at the random and provenance locations were extracted in DIVA-GIS 5.4.

Future climate data was derived from GCM projections of 2050 climate from the HADCM3 and CCCMA models under the A2a emission scenario (IPCC, 2007). This scenario describes a world with continued population growth, slow economic growth, and slow advances in technological solutions (Nakicenovic and Swart, 2000). The coarse GCM outputs were downscaled to 5 km resolution using smoothing (spatial interpolation), and added to the current WorldClim climatic surfaces to provide surfaces of 2050 climate. Climate values at the provenance locations and trial sites were extracted in DIVA-GIS 5.4 from the WorldClim climate grids of present climate, and the CCCMA and HADCM3 model outputs.

2.4. Climate envelope modeling

Maxent is a CEM modeling program which calculates the distribution of maximum entropy for a species within a given area based on observed climate values at locations where that species has been reported, and produces a climate envelope map that consists of probability values for suitable natural habitat (Phillips et al., 2006). Only introduced recently in CEM modeling, Maxent has performed well when compared with other CEM methods (Elith et al., 2006; Graham and Hijmans, 2006), and has been used in several studies to predict species distribution (e.g. Miller and Knouft, 2006; Prates-Clark et al., 2007).

The climate envelope maps that predict natural species distribution under the present climate were evaluated for their accuracy using the ROC Area Under Curve (AUC) statistic. This is a common evaluation method in CEM studies (e.g. Elith et al., 2006;

Phillips et al., 2006). AUC were interpreted following Araújo et al. (2005): AUC near 0.5 are similar to random prediction and indicate poor model performance, AUC above 0.9 indicate excellent model performance.

To predict the climate change impacts, the developed climate envelopes of natural species distribution were projected by Maxent to the future climate models CCCMA and HADCM3. Suitable areas of natural species occurrence were defined following the threshold of when 90 percent of the provenance locations were included in the climate envelope at present climate. To obtain an indication of the predicted impact of climate change on natural species occurrence, we calculated the change in superficies of suitable area and verified with χ^2 homogeneity tests if the proportion of suitable provenance locations significantly changed in 2050 following the predictions from CEM. The probability values of suitable natural habitat at the provenance locations were extracted in DIVA-GIS 5.4 from the grids that were generated by Maxent for the present climate and the future climate models.

2.5. Translocational validation

Validation points were identified for assessing the quality of the predictions in the climate envelope derived from Maxent. These validation points were acquired by correlating CEM-generated suitability values for natural pine occurrence with the observed height and survival at trials established in a present climate that matched respectively with the present climate and predicted future climate at provenance locations. To measure climatic distances between provenance collection sites and field trials, Euclidean distances based on the standardized sub-sampled climate variables were calculated. As a threshold for matching climates, the 10 percent of smallest distances between provenance collection sites themselves was used. When the climate of more than one trial site matched with the climate at a provenance collection site, the average height and survival from those sites was used in the correlation. Provenance collection sites that did not climatically match with trial sites, and vice versa, were not included in the correlation.

Further, we correlated CEM-generated suitability values for natural pine occurrence with the climate conditions at provenance locations and examined if pine performance at the field trials responded in a similar way to these climate conditions. For each species, the suitability values from the CEM predictions under present and the predicted future climates were taken together in one analysis and correlated to the corresponding climate values (suitability values from each CEM prediction are equally related to the sub-sampled climate variables as the CEM calculations are based in all cases on the same climate envelope). To examine if pine performance did relate in a similar way to the climate conditions at the provenance collection sites, the height and survival values from the climatically matching trial sites were correlated to the same climate values as the suitability values were.

2.6. Natural and potential climate ranges of adaptive ability

We conceptualized a simpler version of the climate envelope of natural species occurrence of the two pine species by making two-dimensional relations between the sub-sampled variables. The climate envelopes were bounded by constraints that show the linear combinations of the variable range limits. The climatic ranges in which trial sites were established were compared to the natural climate envelopes to identify the potential climate ranges to which the species is adapted. Climatic differences between provenance collection sites and trial locations were tested with ANOVA.

Table 1

Variable selection for climate envelope modeling of the climate change impact on natural pine occurrence.

Climate variables	R^2 with own cluster	R^2 with next closest cluster	Similarity with random distribution (Mann-Whitney U -test)
<i>P. patula</i>			
Cluster 1			
Annual mean temperature (C°)	0.99	0.21	5.0E–14*
Maximum temperature in the warmest month (C°)	0.89	0.28	4.4E–16*
Minimum temperature in the coldest month (C°)	0.86	0.21	2.0E–06*
Mean temperature in the wettest quarter (C°)	0.95	0.22	1.4E–15*
Mean temperature in the driest quarter (C°)	0.91	0.23	8.9E–12*
Mean temperature in the warmest quarter (C°)	0.94	0.26	7.1E–15*
Mean temperature in the coldest quarter (C°)	0.94	0.30	2.2E–10*
Cluster 2			
Annual precipitation (mm)	0.96	0.25	5.4E–05*
Precipitation in the wettest month (mm)	0.95	0.23	3.0E–04*
Precipitation in the wettest quarter (mm)	0.98	0.32	1.0E–03*
Cluster 3			
Precipitation in the driest month (mm)	0.95	0.17	1.3E–05*
Precipitation seasonality (standard deviation of monthly precipitation values)	0.59	0.22	8.9E–01
Precipitation in the driest quarter (mm)	0.95	0.23	9.9E–05*
Precipitation in the coldest quarter (mm)	0.86	0.32	5.4E–05*
Cluster 4			
Isothermality	0.95	0.19	2.1E–04*
Temperature seasonality (standard deviation of annual mean temperature $\times 100$)	0.95	0.36	4.7E–06*
Cluster 5			
Mean monthly temperature range (C°)	0.82	0.18	2.7E–02*
Temperature annual range (C°)	0.84	0.53	2.5E–06*
Precipitation in the warmest quarter (mm)	0.38	0.17	5.4E–01
<i>P. tecunumanii</i>			
Cluster 1			
Annual mean temperature	1	0.17	7.5E–18*
Maximum temperature in the warmest month	0.96	0.18	7.5E–17*
Minimum temperature in the coldest month	0.95	0.22	2.9E–15*
Mean temperature in the wettest quarter	0.99	0.17	8.7E–18*
Mean temperature in the driest quarter	0.99	0.16	5.5E–17*
Mean temperature in the warmest quarter	0.99	0.23	1.5E–17*
Mean temperature in the coldest quarter	0.99	0.11	2.7E–17*
Cluster 2			
Precipitation in the driest month	0.91	0.17	1.6E–02*
Precipitation seasonality	0.84	0.26	5.9E–02
Precipitation in the driest quarter	0.94	0.18	1.8E–02*
Precipitation in the coldest quarter	0.89	0.24	6.6E–06*
Cluster 3			
Annual precipitation	0.83	0.37	1.3E–03*
Precipitation in the wettest month	0.88	0.20	5.8E–04*
Precipitation in the wettest quarter	0.96	0.23	3.6E–04*
Precipitation in the warmest quarter	0.55	0.38	1.3E–01
Cluster 4			
Isothermality	0.93	0.20	8.8E–02
Temperature seasonality	0.93	0.21	1.6E–01
Cluster 5			
Mean monthly temperature range	0.94	0.18	5.0E–01
Temperature annual range	0.94	0.27	9.2E–01

Hierarchical clustering of the 19 climate variables. R^2 indicates goodness to fit. Significant differences in Mann–Whitney U -tests are indicated with *. From each cluster, the variable that distinguished most significantly natural pine habitat from random distribution is highlighted in grey. These variables were included in the climate envelope modeling and all other analyses.

Finally, we assessed how the climate conditions at the provenance collection sites changed with respect to the potential climate ranges to which the two species are adapted, defined by the climate ranges in which they were established in field trials. A principal component analyze (PCA) was carried out for each species to ordinate based on the sub-sampled climate variables the present and predicted future climate at provenance collection sites

in relation to the present climate at trial sites in Colombia, Brazil, and South Africa. An ANOVA was carried out for each pine species to assess if there were differences between the climatic distances from provenance collection sites to the field trials in Colombia, Brazil, and South Africa respectively, between present climate and the future climate models, and if there was an effect of interaction between countries and climate models on these distances.

3. Results

3.1. Climate variable selection

For each pine species, 5 climate parameter groups were clustered from the initial 19 climate variables to characterize the climate of provenance locations. These groups were different in composition for each species (Table 1). In the case of *P. tecunumanii*, representative climate variables were only selected from the first three clusters, since the last two clusters did not contain any more climate variables that explained significant differences between the natural habitat and the distribution of random locations around the provenance locations (Table 1). The climate variables that best defined the natural habitat of *P. patula* were from each cluster respectively: (1) maximum temperature in the warmest month (MTWARM); (2) annual precipitation (AP); (3) precipitation in the driest month (PDRIEM); (4) temperature seasonality (TSEAS); and (5) temperature annual range (TAR). For *P. tecunumanii* the climate variables that defined best the natural habitat were: (1) annual mean temperature (AMEANT); (2) precipitation in the coldest quarter (PCOLDQ); and (3) precipitation in the wettest quarter (PWETQ). These variables were used in the further analyses.

3.2. Climate envelope modeling

The developed climate envelopes did an excellent job in characterizing the distribution of both *P. patula* (AUC = 0.97) and *P. tecunumanii* (AUC = 0.92) under present climate. The number of

suitable provenance collection sites for *P. patula* decreased significantly under both future climate models (CCCMA: $\chi^2_1 = 5.90$, $p = 0.015$; HADCM3: $\chi^2_1 = 4.77$, $p = 0.03$; Fig. 1). A significant number of suitable provenance collection sites for *P. tecunumanii* was lost under the HADCM3 model ($\chi^2_1 = 6.61$, $p = 0.01$; Fig. 1). Under the CCCMA model only a strong but not significant decline of suitable *P. tecunumanii* provenance locations was observed ($\chi^2_1 = 3.64$, $p = 0.056$; Fig. 1). The area with suitable climate for *P. patula* occurrence decreased under the CCCMA model with 39 percent and under the HADCM3 model with 36 percent. In the case of *P. tecunumanii*, respectively 40 and 49 percent of suitable areas were lost. Hardly any new suitable areas were gained: only two percent suitable *P. tecunumanii* habitat under the HADCM3 model.

3.3. Translocational validation

The CEM-predicted suitability values for natural pine occurrence did not correlate positively with height or survival at climatically similar trial sites (Fig. 2). Instead, several negative correlations were found: between height of *P. patula* at trial sites and suitability values for natural occurrence under the present climate and under the CCCMA model, between height of *P. tecunumanii* at trial sites and suitability values for natural occurrence under the CCCMA model, and between survival of *P. tecunumanii* at trial sites and suitability values for natural occurrence under the present climate and the two future climate models (Fig. 2). In all other cases no significant correlations were found.

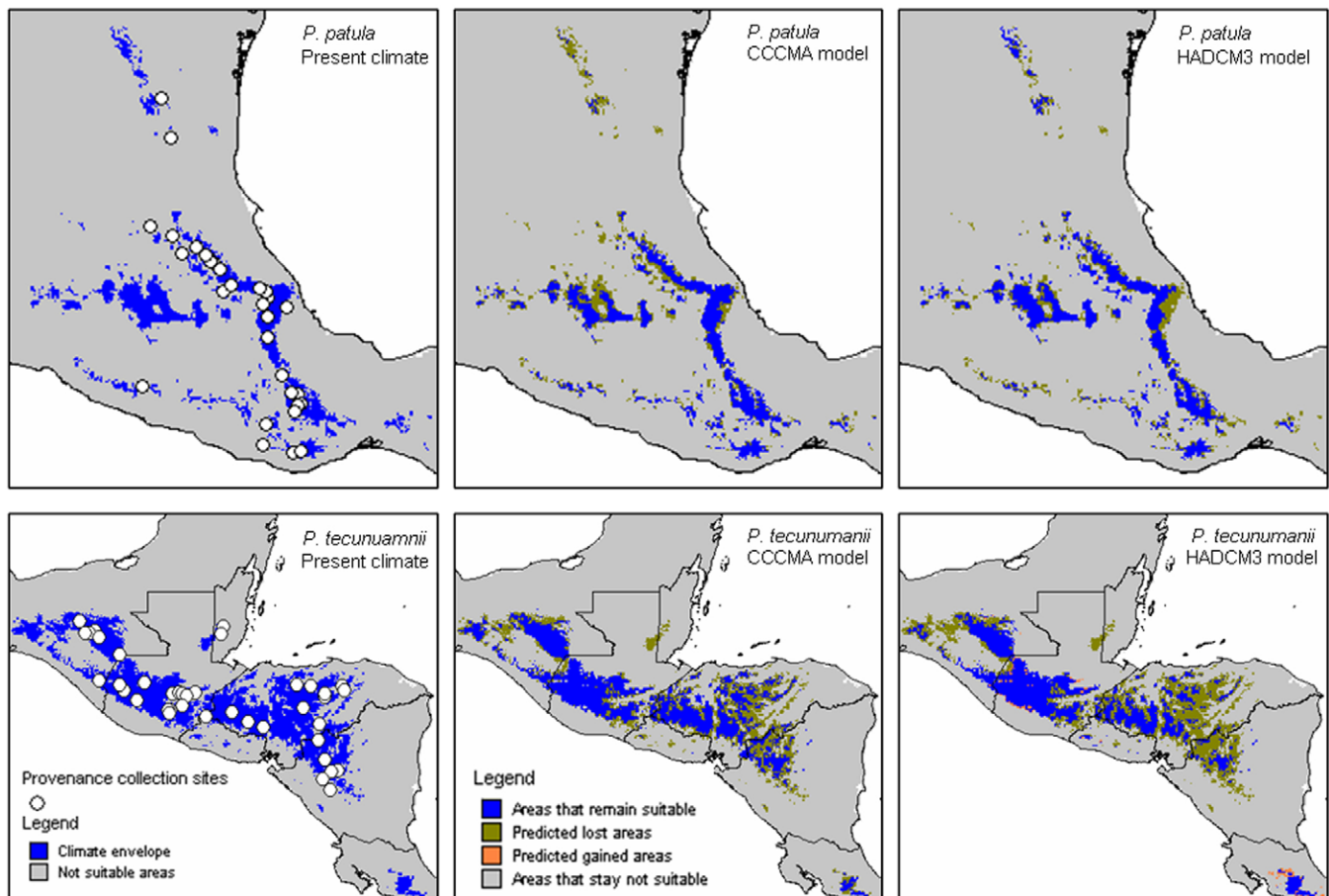


Fig. 1. Climate envelope maps for the natural distribution of *P. patula* and *P. tecunumanii* and the predicted impacts of climate change on their distribution by 2050, developed in the CEM modeling program Maxent. Areas were considered suitable for *P. patula* occurrence above a probability value of 0.248 and for *P. tecunumanii* when this value was higher than 0.267. Only in the case of *P. tecunumanii* under the HADCM3 model new suitable area was gained, but that was only two percent of the total suitable area in 2050.

In most cases, the suitability values for natural occurrence and climatically matching height and survival values correlated differently to the corresponding climate values from the provenance collection sites (Table 2). Suitability values for natural *P. patula* occurrence and matching height values correlated both best with MTWARM, but suitability did so negatively while height positively. Suitability values for natural *P. patula* occurrence correlated also negatively with TAR and TSEAS, while respectively matching height and survival values did so positively. Positive correlation was found between suitability values for *P. patula* natural occurrence and AP and PDRIEM. The suitability of *P. tecunumanii* natural occurrence was correlated highly significant

to AMEANT and POLDQ. While it did so negatively, matching survival and height values were positively correlated to these climate variables. Both suitability of natural *P. tecunumanii* occurrence and matching height values correlated positively to PWETQ.

3.4. Natural and potential climate ranges of adaptive ability

P. patula trials were established in wider TSEAS ranges by Camcore members than *P. patula* normally occurs in its natural habitat (Table 3; Fig. 3). AP and PDRIEM at *P. patula* provenance locations were restricted in comparison to the conditions where

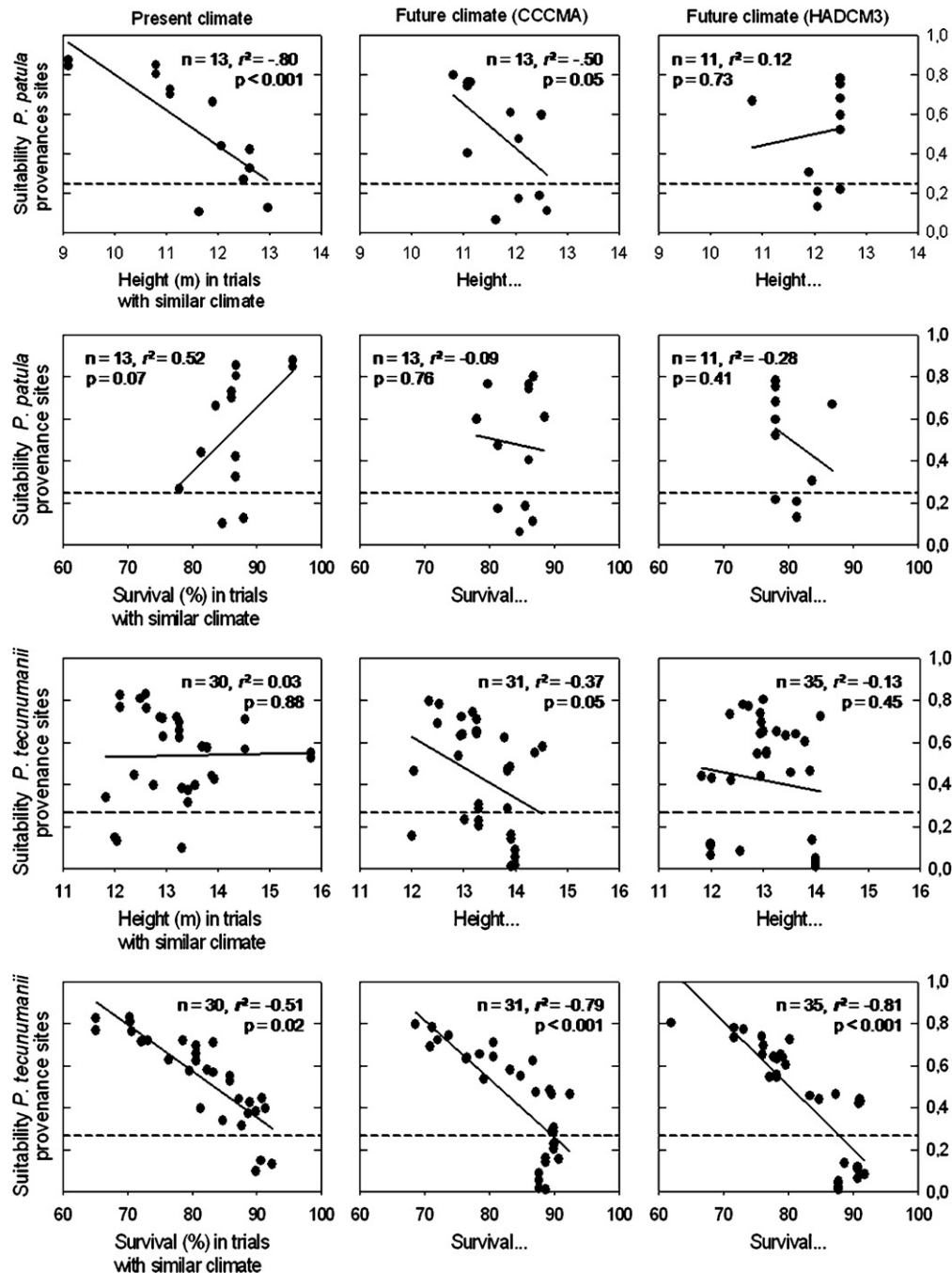


Fig. 2. Correlation of CEM-generated suitability values for natural pine occurrence with the observed height and survival at trials established in a present climate that matched respectively with the present climate and the predicted future climates at the provenance locations in the wild. A regression line is drawn through the points. The dashed line represents the CEM threshold of suitability. Below that line, CEM predicts climate is not suitable anymore for natural pine occurrence. The amount of validation points (n) and Pearson's correlation coefficient (r^2) are given in each graphic plot.

Table 2

Correlation of climate conditions at provenance locations with CEM-suitability values, and height and survival from climatically matching trials.

	Suitability	Height	Survival
<i>P. patula</i>			
MTWARM	−0.88***	0.68***	−0.31
PDRIEM	0.83***	−0.42*	0.19
TSEAS	−0.54***	0.20	0.37*
TAR	−0.84***	0.38*	0.13
AP	0.53***	−0.19	0.11
<i>P. tecunumanii</i>			
AMEANT	−0.96***	0.32***	0.88***
PCOLDQ	−0.34***	0.42***	0.41***
PWETQ	0.25*	0.32**	0.10

P. patula validation points: $n = 37$. *P. tecunumanii* validation points: $n = 96$.

* Significant correlation (Pearson's coefficient) when $p < 0.05$.

** Significant correlation (Pearson's coefficient) when $p < 0.01$.

*** Significant correlation (Pearson's coefficient) when $p < 0.001$.

the species was established in trial sites. No significant differences were found in the distribution of MTWARM and TAR between *P. patula* provenance locations and trial sites. Outlier trial sites indicated that *P. patula* is able to grow under much lower and

higher TAR than would be suggested by its natural occurrence in Mexico. Outlier trial sites were also established under relative low MTWARM, while outlier *P. patula* provenance locations did occur under extreme high MTWARM (Table 3; Fig. 3). At *P. tecunumanii* provenance locations, PCOLDQ was lower than at the trial sites where the species was established by Camcore members (Table 4; Fig. 3). On average PWETQ at *P. tecunumanii* provenance locations was higher than at trial sites although minimum and maximum values of PWETQ were fairly similar. No significant differences were found for AMEANT, but outlier provenance locations occurred in areas with relatively low AMEANT (Table 4; Fig. 3).

P. patula provenance collection sites were most similar to South African trial sites ($F = 113.76$, $p < 0.001$; Fig. 4). Overall taken, climatic distances between *P. patula* provenance collection sites and trials did not change in future models ($F = 0.31$, $p = 0.73$). But climate distances differed between countries depending on the climate model ($F = 4.1$, $p < 0.001$). *P. patula* provenance collection sites became under both future climate models more similar to the present climate at South Africa sites and in contrast became more distant to the present climate at Colombian sites (Fig. 4). At present, *P. tecunumanii* provenance locations climatically resembled most to Brazilian trials ($F = 1215$, $p < 0.001$; Fig. 4), and became even more similar to these trials in the future climate

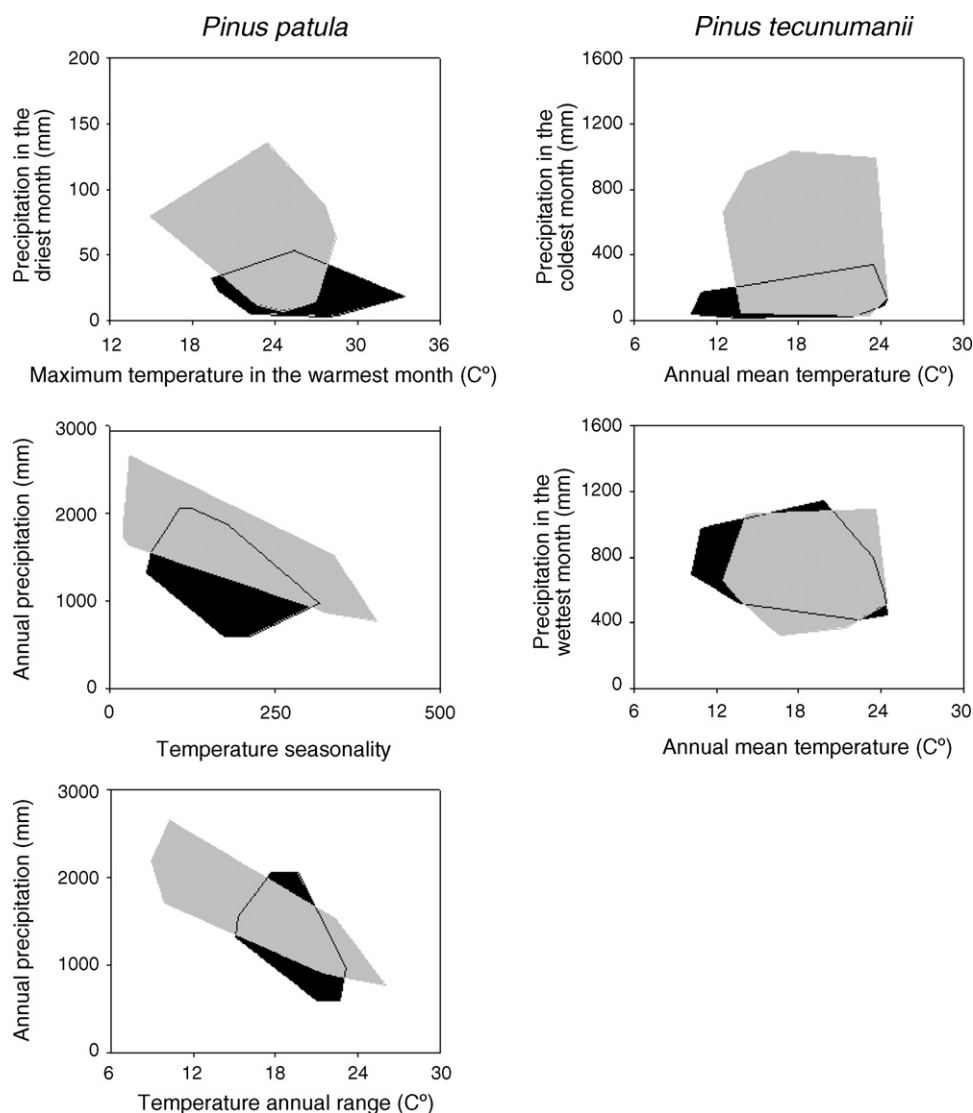


Fig. 3. Simplified climate envelopes for natural pine habitat (in black) and the climatic ranges in which the field trials were established (in grey), presented by two-dimensional linear combinations of variable range limits. Temperature seasonality: standard deviation of annual mean temperature $\times 100$.

Table 3Differences in climate ranges between *P. patula* provenance locations in the wild and field trials.

Climate variables	MTWARM		PDRIEM***		TSEAS*		AP*		TAR	
Sites	Wild	Trials	Wild	Trials	Wild	Trials	Wild	Trials	Wild	Trials
Mean	24.4	24.9	18.6	62.6	165	225.6	1215.3	1466.7	19.7	18.3
SD	3.1	2.9	10.5	39.5	57.8	130.5	375.2	479.5	2.1	4.9
Minimum	19.4	14.9	3.0	7.0	56.9	20.5	590	774	15.1	9.0
Maximum	33.4	28.4	53	135	317.9	404.7	2059	2658	23.2	26

Wild (provenance collection sites): $n = 31$. Trial sites: $n = 28$. SD: Standard deviation.* Significant differences in ANOVA when $p < 0.05$.*** Significant differences in ANOVA when $p < 0.001$.**Table 4**Differences in climate ranges between *P. tecunumanii* provenance locations in the wild and field trials.

Climate variable	AMEANT		PWETQ***		PCOLDQ***	
Sites	Wild	Trials	Wild	Trials	Wild	Trials
Mean	18.8	18.5	694.7	565.3	130.3	284.7
SD	3.7	2.7	155.8	200.4	90.9	317.8
Minimum	10.2	12.5	419	323	17	30
Maximum	24.5	24.5	1144	1092	340	1026

Wild (provenance collection sites): $n = 41$. Trial sites: $n = 34$. SD: Standard deviation.* Significant differences in ANOVA when $p < 0.05$.*** Significant differences in ANOVA when $p < 0.001$.

models, especially under the HADCM3 model, but became more distinct to the present climate in South African and Colombian trials ($F = 10.10$, $p < 0.001$; Fig. 4).

4. Discussion

It is argued that CEMs overestimate the impact of climate change on tree species (Kremer, 2007; Botkin et al., 2007). Validation of CEM results for future climate change is identified as a research priority (Dormann, 2007; Thuiller et al., 2007). We used a series of international provenance trials as a mean of validating CEM climate change impact predictions on natural pine occurrence. Predictions from CEM suggest a big impact by climate change on the natural occurrence of both pine species. More than a third of the actual suitable area is predicted to be lost by 2050 for both species under both GCM models and hardly any new suitable areas were gained. Based on the results from CEM, the number of suitable provenance collection sites is expected to decrease significantly, except for *P. tecunumanii* under the CCCMA model, although in that case there was still a clear tendency in decline. The outcomes of the translocational validations however suggest that natural stands of *P. patula* and *P. tecunumanii* have a broader adaptation to climate change than CEM predicts. The results from the field evaluations

showed that the pines species perform well in a wider range than the limits of the climate envelopes developed by CEM.

4.1. Climate variable selection

With the help of the variable clustering and the Mann–Whitney *U*-test, the number of variables for the analyses of *P. patula* was reduced to five, and in the case of *P. tecunumanii* to three variables. The method does not pretend to identify causal environmental factors for species occurrence, but given the lack of plant physiological and phenological parameters, we consider this to be a valid method to select variables for CEM predictions, minimizing redundancy and selecting the variables that best define the current geographic distribution.

4.2. Translocational validation and adaptive ability to changes in climate

The CEM-generated suitability values for natural species occurrence did not correlate positively with height and survival from climatically matching field trials, and in several cases they were negatively correlated. Such contrary responses were also observed when suitability values and matching height and survival values were correlated to the same climate values from the corresponding provenance collection sites. For instance, suitability values for natural species occurrence were negatively correlated to increasing temperature whereas matching height and survival values were positively related to that increase. This suggests that despite the negative CEM predictions the species are adapted to the foreseen temperature increment in their natural habitat.

In the case of several climate variables, the two pine species performed well in wider ranges than those found in their natural habitat. For instance, successful establishment of trial sites of *P. patula* outside normal climatic boundaries that characterize its occurrence in Mexico indicates that this species is adapted to much wider ranges of temperature seasonality (TSEAS) than found in its natural habitat. *P. tecunumanii* appeared to perform well under

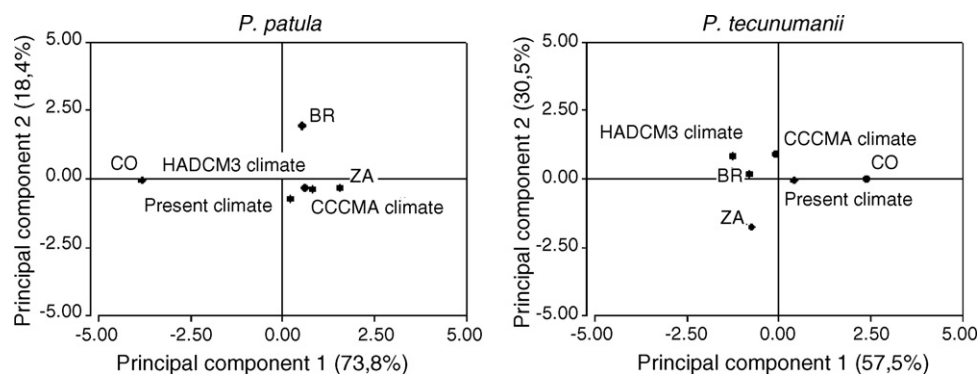


Fig. 4. Ordination with the help of principal component analyses (PCA) of average present climate and future climates (HADCM3 and CCCMA model) of provenance collection sites and the average present climate of field trials established in South Africa (ZA), Brazil (BR) and Colombia (CO) respectively.

precipitation patterns different from its natural habitat. Due to the wide ranges of adaptability it can be expected that wild pine stands are able to persist substantial changes in climate. These results are in line with similar studies. Four *Rhododendron* tree species, native to the Himalayas, proved to survive well at higher temperature values than occur in their natural niches (Vetaas, 2002). Miller and Knouft (2006) found that natural populations of the fruit tree *Spondias purpurea* in Middle America occurred in a relatively narrow niche of marginal areas, whereas this species was successfully introduced in much wider climate ranges.

In general, the length of the growing season (temperature) has a positive effect on tree development (Aitken et al., 2008). Often tree species are more tolerant to high temperatures than to minimum temperatures (Vetaas, 2002). But it is difficult to assess to which limit tree species can tolerate or respond positively to high temperatures (Saxe et al., 2001). This depends also on the effect of the combined changes in temperature and precipitation (Aitken et al., 2008).

In the case of *P. patula*, the climate ranges in which field trials were established did not cover the hot and relatively dry conditions where some outlier provenance locations occur in the wild. It would be relevant to learn how *P. patula* performs under these conditions and include that information in the validation of climate change impact predictions. Climate change impact studies done for other tropical and subtropical pine species show that the performance of those pines is affected negatively by such conditions (Koskela, 2001; Sáenz-Romero et al., 2006). It can be expected that a combination of temperature increment and drought has also a negative impact on the growth and survival of *P. patula* and *P. tecunumanii* and consequently on the natural occurrence of these species.

Yet the 2050 climate of the *P. patula* provenance locations is predicted to become on average more similar to the present climate of South African field trials where the species successfully was established. In the case of *P. tecunumanii*, climate at the provenance locations is predicted to become closer to the present climate at Brazilian sites. These results suggest that trees of wild *P. patula* and *P. tecunumanii* stands are sufficiently adapted to acclimatize to the new ecological climate niches at their locations defined by the predicted climate conditions in 2050.

4.3. The role of climate and other factors in changes of natural species distribution

Besides the broad adaptation found for the pine species in our study, the reason that pine performance at trial sites did not concur with the CEM-predicted climate change impacts on natural species occurrence may be due to climate is not the only factor that shapes the natural geographic ranges of natural pine areas. In fact, to what extent climate determines changes in natural species distribution and the role of other factors like biotic interactions and dispersal ability are important points of discussion in climate change impact studies on natural species distribution (Pearson and Dawson, 2003).

Biotic interactions, such as competition, were not taken in account in the translocational validation of natural species occurrence with the results from field trials. Camcore trials are managed under favorable conditions (fire and weed control) while in their natural habitat competition with other tree species is likely to limit pine distribution. This implies that successful pine growth and survival at trial sites tend to overvalue suitable areas for natural species occurrence.

To what extent stands of tree species are to be pushed out by competition with other tree species at their actual locations during the expected climate changes in the next 50–100 years, depends on the ability of climatically better suited tree species to invade these locations. But invasion by better suitable tree species is often

substantially delayed by dispersal limitations of these species (Svenning and Skov, 2004; Kramer, 2007). Further do trees prolong their existence in changing ecosystems because of their longevity (Hamrick, 2004). It can be anticipated that most tree species not going to be driven out by other tree species before climate severely weaken them. In case of the pine species in our study, the climate in their natural habitat is predicted to become closer to several areas where the species perform well at the trial sites, which makes it even less likely they will be pushed out by other tree species.

A factor of importance for these pine species is the frequency and intensity of fires. Both *P. patula* and *P. tecunumanii* are closed-cone pines. They have developed in an environment where fires have greatly affected patterns of evolution and play an important role in the dynamics of recruitment and mortality for these species (e.g. Rodríguez-Trejo and Fulé, 2003; Styles and McCarter, 1988). The present day natural range of both species might not reflect historic occurrences. To provide more insight into the impact of climate change on future regenerations of these pine species, the impact of climate change on these fire events should be understood and included in the predictions of climate change impact on natural species distribution. As an example, high frequency of fires in the mountains of Central America would favor *Pinus oocarpa* over *P. tecunumanii*. *P. oocarpa* has evolved to produce sprouts from the base of its stem after fires as a survival mechanism while *P. tecunumanii* has not (Dvorak et al., 2001; Dvorak, 2002).

Climate change is also likely to influence the occurrence of forest pest outbreaks. This has not been included in our analysis but this could have a potentially high impact on the natural distribution of the pine species in our study. Billings et al. (2004) report that between 1999 and 2003 about 90,000 ha of pine forests from Central America were killed by bark beetles, including *P. tecunumanii* stands. The outbreak was preceded by intense wildfires and extent droughts caused by the climate dynamics of El Niño Southern Oscillation (Billings et al., 2004). This demonstrates how extreme climate events can trigger pest outbreaks. There are strong indications that recent pest outbreaks killing large areas of temperate pine forests in Canada have happened because of a temperature increment that is related to global climate change (Kurz et al., 2008). CEM modeling can help assessing the risk of these outbreaks under the foreseen changes in climate (Logan et al., 2003).

4.4. Genetic variation

Dormann (2007), Kremer (2007) and Aitken et al. (2008) stress the importance to include genetic variation in predictions of climate change impact on natural species distribution. We assumed in our validation methods that trees from different wild pine species stands will respond in a similar way to climate change. However, trees from genetically divergent stands are expected to respond differently to changes in climate conditions. Indeed, in many fitness-related provenance tests for tree species, provenances perform differentially under similar climate conditions (e.g. Rehfeldt et al., 1999, 2002). The difference in provenance performance from best to worst for productivity across a number of environments for *P. tecunumanii* in the Camcore testing program is approximately 30 percent (Hodge and Dvorak, 1999). This trend has been found for a number of other tropical and subtropical pines (e.g. Hodge and Dvorak, 2001).

For some pines species, adaptation to new environments is apparently very rapid. *P. patula*, originally sampled in Mexico, grown in South Africa for one generation, and returned to Mexico, grew faster than local sources, but was more susceptible to cold attacks (Saenz-Romero et al., 1994). Fast adaptation have been reported for several other pine and conifer species (see Saxe et al., 2001; Kremer, 2007; Aitken et al., 2008), but the mechanisms behind are

unfortunately not fully understood (Aitken et al., 2008). There are high expectations from combining population genetics with climate change modeling (Davis and Shaw, 2001; Thuiller et al., 2007), but more research must be carried out to better understand adaptation mechanisms at the genetic level (Kremer, 2007).

4.5. Conservation implications

Immediate-term threats might require more urgent action to ensure the long-term protection of these pine species, when compared to the long-term threat of climate change. At the moment for many natural pine populations in Mexico and Central America no effective conservation measurements exist. Sáenz-Romero et al. (2003) for instance, propose the establishment of a network of *in situ* forest genetic resources conservation units to protect the genetic variation of Mexican pine species against immediate-term threats like fragmentation and deforestation. *P. tecunumanii* is already under threat in Central America and southern Mexico and is classified as vulnerable according to the criteria of IUCN (2007) and some populations are critically endangered (Dvorak et al., 2000a). Human pressure is likely to continue to be high since this species occurs naturally in areas that suit agriculture and urbanization (Styles and McCarter, 1988). Among possible measurements to protect *P. tecunumanii* provenances, conservation parks outside its natural distribution range are currently being planned in South Africa and other countries by the Camcore membership (Camcore, 2005). CEM modeling can help identifying areas for these conservation parks that are suitable and remain low-impacted by climate change.

The time scope of our study is until 2050. It can be anticipated that in the second half of the 21st century the climate in the natural pine areas moves further away from the present climate and that pine provenance locations will become more seriously affected. Further climate modeling in combination with research on the performance of the pine species under the predicted climate conditions after 2050 can contribute to a better understanding of the implications of climate change for natural pine occurrence on such a long-term time scale.

5. Conclusions

CEM predictions suggest significant impacts of climate change on the natural species distribution of the two pine species. The pine species however demonstrate they can perform well in a wide range of climates, including conditions that are predicted by CEM as unsuitable for natural pine occurrence. The climate conditions where the two pine species naturally occur are expected to become in the future closer to the present climate of some areas where the pine species are successfully established in field trials. These findings suggest that the pine species are in their natural habitat better adapted to climate change than is predicted from CEM. The outcomes of CEM climate change impact predictions should therefore be interpreted with caution. In the short term, fragmentation by urbanization and agriculture seem to be more urgent threats for the vulnerable species *P. tecunumanii* than climate change.

Translocational validation can give already more insight into the adaptive ability of tree species populations to climate change. The inclusion of factors other than climate, in climate change modeling will help us better understand the distribution dynamics of tree species in changing environments. Such factors are invasion by better suited tree species, disturbance events like fire occurrences and pest outbreaks, and genetic variation.

Translocational validation can be applied to other tree species for which large provenance $\times$ environment experiments exist. These experiments exist mostly for temperate and boreal forest

species of the northern hemisphere but more data is becoming available for tree species from tropical and subtropical regions (Gapare et al., 2001; Kanzler et al., 2003). This opens the way for a better assessment of climate change impact on subtropical and tropical tree species.

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