Schadensanfälligkeit und Anpassungsfähigkeit von Kiefernplantagen in den Tropen und Subtropen im Kontext des Klimawandels

Dissertation

Zur Erlangung der Würde des Doktors der Naturwissenschaften

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To whom it may concern,

I declare that the use of the English language in Christoph Leibing's PhD report is meeting the general quality requirements for scientific publications.

Kind regards,

Cali, Colombia, 1st July 2013

Andy Jarvis | Place, Date

Program Leader of the Decision and Policy Analysis Program in the International Centre for Tropical Agriculture (CIAT) and
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PhD report synopsis

Introduction: There is large consensus in the scientific community that climate change is one of today's most important global challenges. The survival of many valuable ecosystems is at risk and especially forested ecosystems will be struggling to keep pace with the rapid alteration of their environment. Their long generation cycles and slow migration rates make them particularly prone to be negatively affected by rapid changes.

Justification: I summarize and discuss in this report three studies that examined how two important plantation species, *P. patula* and *P. tecunumanii*, may be affected by climatic changes at natural stands and locations where the species are planted. There exists an increasing need to assess and optimize the way we use available forest genetic resources in order to sustain stable growth rates in future rotations. Climate change may not only lead to reduced yields where the species are planted but may also pose a possible threat to the species' natural populations.

Hypothesis: The hypothesis tested in this research are the following: (1) Climate envelope models coupled with results from provenance trials can assist in the determination of a species' capacity to withstand the adverse effects of climate change and (2) site quality models based on field trial data can help to maintain plantation productivity and improve our understanding of tree species' adaptation to a changing climate when coupled with high resolution climate data.

Methods: We investigated the impact of climate change on natural populations of *P. patula* and *P. tecunumanii* via climate envelope modeling and assessed the adaptive ability of the two pine species based on growth data from large provenance trials.

Content: This report introduces and discusses the implications of outcomes from three studies published in a time span from 2009 to 2013. The studies were published in three different scientific journals: "Forest Ecology and Management", "Scandinavian Journal of Forest Research", and "Forests". The first publication from 2009 assesses climate change impact prediction on P. *patula* and *P. tecunumanii* natural populations. The second and third publication focuses on planting sites and investigates climate related differences in growth performances on subspecies and provenance level.

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Abbreviations

Additive Mean Effect and Multiplicative Model	AMMI
Analysis of Variance	ANOVA
Area Under Curve	AUC
Canadian Centre for Climate Modelling and Analysis	CCCMA
Central America and Mexico Coniferous Resource Cooperative	CAMCORE
Centro Internacional de Agricultura Tropical	CIAT
Clean Development Mechanism	CDM
Climate Change, Agriculture, and Food Security	CCAFS
Climate change	CC
Climate Envelope Modeling	CEM
Conference of Parties	COP
Decision and Policy Analysis	DAPA
Diameter at Breast Height	dbh
Forest Genetic Resources	FGR
Free Air Carbon Dioxide Enrichment	FACE
General Circulation Model	GCM
Genetic Algorithm for Rules Set Production	GARP
Genetic by Environment Interaction	GxE
Geographic Information System	GIS
Gesellschaft für International Zusammenarbeit	GIZ
Gesellschaft für Technische Zusammenarbeit	GTZ
Hadley Centre Coupled Model, version 3	HADCM3
Intergovernmental Panel on Climate Change	IPCC
International Union for Conservation of Nature	IUCN
Multiple Linear Regression	MLR
Pinus patula var. longipedunculata	LONGIP
Pinus patula var. *patula*	PAT
Pinus tecunumanii high elevation population	HIGH
Pinus tecunumanii low elevation population	LOW
Receiver Operating Characteristic	ROC
South African Pulp and Paper Industries	SAPPI
Species Distribution Model	SDM
Variance inflation Factor	Vif

1. Introduction

The anthropogenic alteration of precipitation and temperature patterns is likely to be one of the most important global challenges faced by ecosystems and societies alike (O'Neill & Oppenheimer, 2002; Parmesan, 2006; Walther, Hughes, Vitousek, & Stenseth, 2005). The scientific basis for this "man-made" climate change is established (Solomon, 2007) and evidence is mounting that especially forested ecosystems will be profoundly affected (Hamrick, 2004; Köhl et al., 2010; Saxe, Cannell, Johnsen, Ryan, & Vourlitis, 2001). Important plantation tree species are likely to be negatively affected in their natural habitat (Dvorak, Hodge, & Payn, 2008) and locations where species can be grown as exotics will have to be adjusted. Despite the importance of climate change for the growth and survival of these tree stands, considerable uncertainty still exists on how different species and genotypes will respond to changes in climate (Botkin et al., 2007; Kremer, Koskela, Buck, & Cros, 2007). Climate change is predicted to rapidly alter growing conditions in an unprecedented way and will force foresters to make decision under considerable uncertainty (Noss, 2002; D. L. Spittlehouse, 2005). In combination with anthropogenic stressors such as pollution, habitat fragmentation, land-use changes, invasive plants, animals, and pathogens, and altered fire regimes climate change demands for a novel approach to sustainable forest management. If left unaltered forest ecosystems will likely not be able to maintain their productivity and may become more susceptible to undesirable changes (Millar, Stephenson, & Stephens, 2007).

Climate envelope- and site quality models can help to indicate a way for the forestry sector to adequately cope with the rapid alteration of growing conditions. Model results coupled with Geographic Information Systems (GIS) are a widely-used tool to assist the management of forest resources in an uncertain environment. A common approach assesses the potential climate change impact on natural populations based on the results of climate envelope models (CEMs) (Gómez-Mendoza & Arriaga, 2007; Hamann & Wang, 2006; Iverson & Prasad, 1998; Leibing, van Zonneveld, Jarvis, & Dvorak, 2009; Pearson & Dawson, 2003). The current geographic distribution of a species is used to build a model of most suitable climate conditions for natural species occurrence. This so called climate envelope aims to describe the species' ecological niche and can be projected into the future on the basis of results from general circulation models (GCMs). The outcome is a geographical indication of where species gain or lose suitable habitats (cf. figure 1). However, the extent to which trees can withstand environmental changes at their actual locations remains largely understudied in these CEM based climate change impact studies (Thuiller et al., 2008).

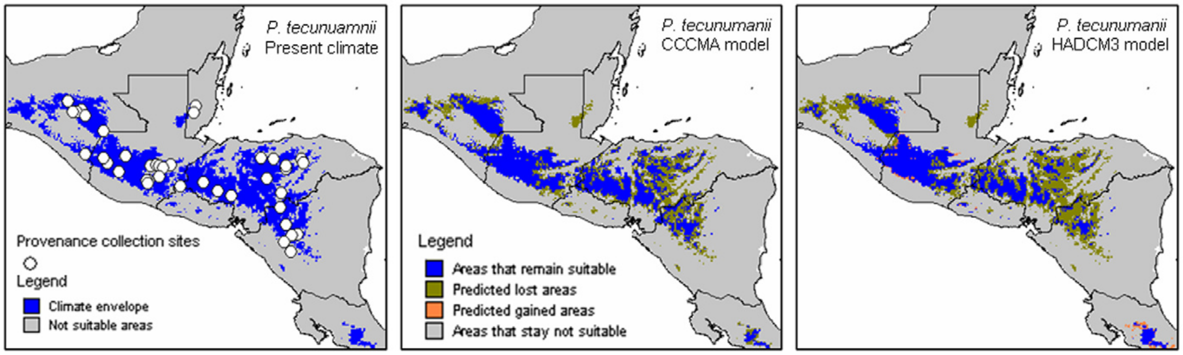


Fig. 1. Climate envelope maps for the natural distribution of *P. tecunumanii* and the predicted impacts of climate change on their distribution by 2050. Adapted from van Zonneveld et al., 2009

But climate change is not only challenging a species' persistence at its' natural locations. Since climate is changing rapidly, it may also become increasingly difficult to choose the right species and provenance to plant where species are introduced as exotics.

1.1. Research objectives

The objective of the first of three studies presented and discussed in this report was to evaluate if CEM can reliably assess the impact of climate change on the persistence of natural populations of *Pinus patula* and *Pinus tecunumanii* at their actual locations. If successful this model could help to inform about conservation measures with the aim to protect the species in their natural habitat. In a second step we developed decision support models that (1) predict the impact of climate change on wood productivity at locations where the pines are planted as exotic and (2) identify what kind of tree should be planted today that will be resilient to climate changes 10 or 20 years in the future.

1.2. Camcore provenance trial data

The three studies discussed in this report were conducted at the International Centre for Tropical Agriculture (CIAT) Cali, Colombia in cooperation with the International Tree Breeding and Conservation Program (Camcore) at North Carolina State University. Camcore's data set of 153 geo-referenced provenance trials, established in Colombia, Brazil and South Africa during 1981 and 1997 formed the data basis of all analyses (figure 2). This dataset of provenance trials was complemented by coordinates of 24 provenance locations in the wild of *P. patula* and 41 provenance locations of *P. tecunumanii* from seed collections provided by Camcore.

The cooperation between Bioversity International, CIAT, and Camcore started in April 2007 with my stay as visiting researcher for Bioversity International. The provenance trial database which formed the principal basis of the collaboration is in its extent and coherence unique in the field of forestry research. All 153 trials were measured for height growth [m], diameter at breast height (dbh) [cm] and survival rate. It is important to note that site and stand management, such as site preparation, spacing of trees, weed control, thinning, and pruning was for all provenance trials as similar as practical in the field. Trial coordinates were carefully checked following the suggestions from Hijmans (1999).

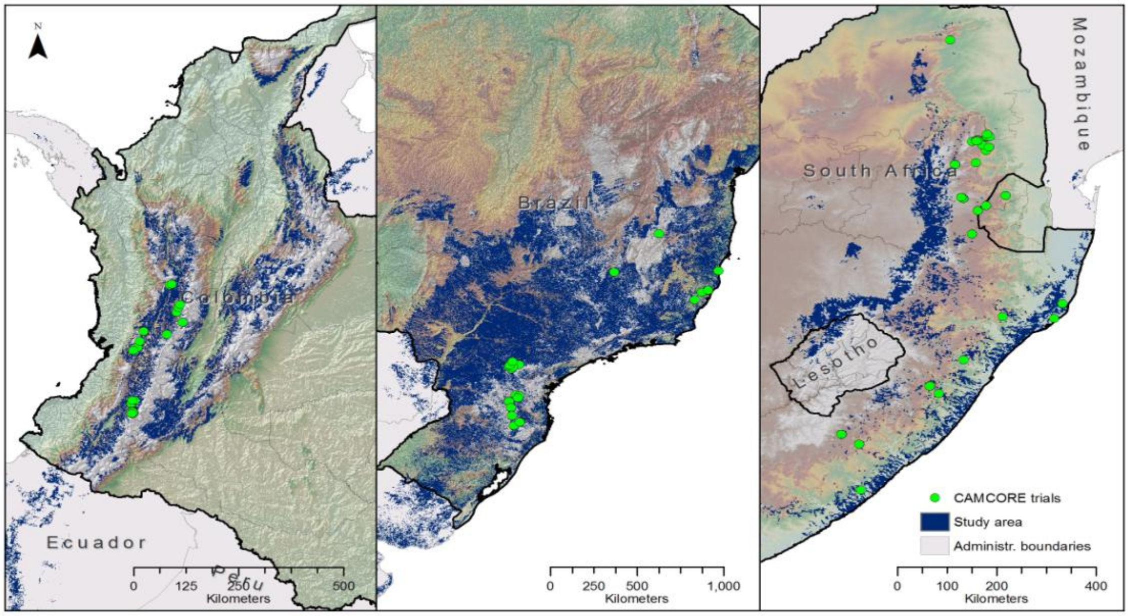


Fig. 2. Map of location of Camcore provenance trials. Adapted from Leibing et al., 2009

1.3. Report structure and overview

This cumulative PhD report summarizes and reflects on implications of the findings of three research projects (Leibing, Signer, van Zonneveld, Jarvis, & Dvorak, 2013; Leibing et al., 2009; van Zonneveld, Jarvis, Dvorak, Lema, & Leibing, 2009). Together these projects shed light on the vulnerability and adaptive capacity of two important pine plantation species, *Pinus patula* and *Pinus tecunumanii*. In a first step we analyzed the impact of climate change on stands where the species naturally occurs. In the two subsequent steps we investigated the vulnerability of productive forest plantations to climate change in terms of achievable growth rates.

I will review the methodology, key findings and implications that can be drawn from each of the three published studies. In this report a close look will be taken on the current state of research the two main fields which are relevant for the publications: (1) Climate envelope modeling and (2) Site quality- and forest growth modeling.

The **first study**, which was published in January 2009 in the journal “Forest Ecology and Management”, describes the ecological niche of the two Mexican and Central American pine species. By projecting the results of climate envelope modeling into the future, the impact of climate change on the persistence of the natural population of these species at their actual locations was estimated. Model results were then used to inform about appropriate conservation measures (van Zonneveld et al., 2009). The **second study** was published in December 2009 in the “Scandinavian Journal of Forest Research”. Here we assessed the need to adapt the choice of seed material for forest plantations under changing climate of two *P. patula* varieties (*P. patula* var. *patula* and *P. patula* var. *longipedunculata*) and two *P. tecunumanii* ecotypes (highland and lowland). The study area comprises planting sites in Brazil, Colombia and South Africa (Leibing et al., 2009). The final and **third study** made use of a statistical analysis tool called *Analogue* which was developed by the Climate Change, Agriculture, and Food Security Program (CCAFS) in collaboration with the University of Reading in 2011 (Ramírez-Villegas et al., 2012). The manuscript was published in March 2013 in the scientific journal “Forests”. The study’s focus lies on the evaluation of growth performance of plantings in Colombia, Brazil and South Africa. With the help of the climate analogue tool we correlated the provenance trials’ height growth to the degree of climatic dissimilarity between planting sites. The outcome of this analysis served as a measurement for the suitability of seed material under a changing climate for four *P. patula* provenances and six *P. tecunumanii* provenances (Leibing et al., 2013).

1. Current state of research

The last decade has seen very lively activity in the field of research on climate change impacts on the exploitation of forest genetic resources (FGR). Much of the interest focuses on the direction of impact predictions regarding FGR’s vulnerability to climate change in natural forests and forest plantations (Loo, Fady, Dawson, Vinceti, & Baldinelli, 2011). Scientists’ opinion vary on the consequences of the rapid environmental changes for FGR (Hamrick, 2004). Some consider that many trees have sufficient phenotypic plasticity and genetic diversity at the population level to significantly reduce the negative effects of climate change, others have taken a different viewpoint and predict severe negative impacts (Koskela, Buck, & Teissier du Cros, 2007; Rehfeldt, Wykoff, & Ying, 2001). Different positions relate partly to the types of species and environments being considered but also result from the difficulties to quantify the extent of phenotypic plasticity in a studied species. In general scientists who make the more pessimistic forecasts often base their views on tropical trees (Dawson et al., 2011) or on temperate species that grow on distribution margins (Mátyás, Vendramin, & Fady, 2009). More optimistic authors tend to make temperate and boreal taxa their object of research. Boreal and temperate ecosystems are expected to benefit from higher temperatures. In these regions today’s low temperatures and long winters are among the most important limiting abiotic growth factors (Lindner et al., 2010).

Any study on forest yields needs information on tolerance and adaptability of tree species. A vital step in the process to create forests that are well adapted to their environment is to find the right genotype to plant at a certain site. This step includes not only choosing the adequate species but also the identification of the best genotypes within a species for a specific environment (Kanzler, 2002). The correct choice of species and seed source represents a vital decision in the process of sustainable forest management and is indispensable to realize gain from plantation forestry (Zobel & Talbert, 1984). However, in the context of an unstable and rapidly changing environment the exercise to choose the right tree to plant becomes more and more difficult.

1.1. Genotype-environment interactions

In order to take the right planting decision a forester needs to know about the differences in climate tolerance among- and within tree species. In other words the so called genotype-environment interactions (GxE) have to be assessed. Many and sometimes complex definitions of GxE exist which can all be reduced to one practical implication: an optimal population or individual on one site is not necessarily the best for the others (Barnes, Bunrsr, & Gibson, 1984). Most of the scientific work which provided the statistical methods to assess the extent of GxE has been conducted in the 60's 70's and 80's; most prominently by the researchers Freeman (1973) and Shelbourne (1973). This report will not give a detailed summary of all the available techniques but rather provide a brief overview on this important facet of FGR and climate change impact studies. The work to summarize the most prominent statistical approaches was undertaken by Kanzler and the following description draws from the review of techniques given in his PhD thesis (Kanzler, 2002).

1) Ranking entry means and phenotypic correlations

A helpful first step to assess GxE is to use simple comparative techniques. This will show if there are any rank changes of entries under different environments. A look at entry means across environments can be helpful. If there are rank changes or differences in relative performance of entries under different environments this may be first evidence of GxE.

2) Analysis of Variance

The analysis of variance (ANOVA) is usually the most widely used technique in any GxE study. It allows the partitioning of total phenotypic variation into components due a) genotype b) environment c) GxE interaction and d) error. Since interactions may result to be statistically significant but need more analysis for better interpretation, an ANOVA can be considered the basis for further data examination.

3) Regression Analysis

In the technique of regression analysis the genotypic means of each site are regressed against the mean value of an environmental effect at each site. We will review this technique in somewhat more detail since it is of specific relevance for the third publication "Selection of Provenances to Adapt Tropical Pine Forestry to Climate Change on the Basis of Climate Analogs" (Leibing et al., 2013).

Finlay and Wilkinson developed in 1963 a methodology to assess the stability of genotypes across environments for 277 barley varieties. In a comparison with several other methods, it produced similar results and in addition it proved advantageous because it allowed for the prediction of performance in an untested environment (Barnes, 1984). The method calculates the linear regression of one variety's yield in a given environment on the mean yield of all varieties in that environment. This allows each genotype to be classified into one of four groups; a) high yielding, stable genotypes (high genotypic means with regression coefficients $b1 < 1$); b) high yielding, unstable genotypes (high genotypic means with $b1 > 1$); c) low yielding, stable genotypes (low genotypic means with $b1 < 1$) and d) low yielding, unstable genotypes (low genotypic means with $b1 > 1$) (Finlay & Wilkinson, 1963). As stated in the article published in Forests in 2013, the underlying idea of this method is that an unstable entry could have higher yields than the more reliable stable source in certain locations. The breeder has to decide if it is better to choose stable or unstable genetic entries for the tree improvement program. Especially with keeping climate change in mind a forester's choice may very well turn in favor of the lower yield but more reliable source ($b1 << 1$).

4) Stability Analysis

Further work following the aim to quantify genotype's stability across environments led to a calculation of a 'stability variance'. This metric is calculated by partitioning the GxE into a number of components, one corresponding to each genotype. The sum of within and between environmental variance for each genotype defines the 'stability variance'. When this latter parameter is equal to the within environmental variance the genotype can be classified as stable (Shukla, 1972).

5) Genetic correlations

Genetic correlations among traits indicate the extent to which one trait will change as a result of a change in another trait (Zobel & Talbert, 1984). This approach has been extensively discussed in the forestry science literature and has been widely used in forestry experiments. It is found to be a useful tool to quantify the role of environments in generating interactions.

6) Multivariate Methods

These methods include principle component, principle coordinate analysis, Additive Mean Effect as well as Multiplicative Model (AMMI). AMMI widely used in agricultural studies did not really bring any new insight in forestry experiments. This is expected to be due to the fact that this technique requires many sites which are often not available in forestry experiments.

We prepared the ground now to step into the two research fields that are most relevant for the work published on the basis of Camcore's provenance trial data. In the following two sections I will give an overview over the current state of research in the two fields that form an integral part of today's research efforts to make forests less vulnerable to climate change. This is 1) The science of **clime envelope modeling** and its applications for climate change impact studies and 2) **Forest growth predictions and site quality modeling** that aim to give decision support for forest managers under uncertain future climate conditions.

1.2. Climate envelope modeling

Ecological niche modeling or climate envelope modeling is a rather new technique that evolved with the availability of fast enough computers in the late 1980s. Aim of this research discipline is to identify priority areas for conservation, keep seed choice adaptable by conserving a species biodiversity in the wild and identify suitable sites for ex-situ conservation. Model results can also be used to describe the potential spread of invasive species once introduced to a new area or to estimate the distance between fundamental and realized niche of a certain species (Heikkinen et al., 2006; R. Hijmans & Graham, 2006). One of the most prominent studies in the field of climate envelope modeling was published in 2004 by Thomas et al. in Nature (Thomas et al., 2004). Their work was cited more than 3,000 times and assessed the projected extinction risk from climate change of a number of different species on 20 % of the earth's terrestrial surface.

Climate envelope models (CEMs) commonly work with data on species presence, so called presence only data. This geo-referenced data of species occurrence once carefully validated (R. Hijmans & Schreuder, 1999) serve as the basis to define a species' ecological niche and therefore the environmental space we assume the species is able to occupy. Based on this space a species' geographic distribution for the current, past or future climate is predicted.

1.2.1. Maxent

There are many CEMs available today but we will put special focus on one particular model which was used by van Zonneveld, et al. (2009) to predict the geographical distribution of *P. patula* and *P. tecunumanii* (figure 3). In 2006 Philips et al. (Phillips, Anderson, & Schapire, 2006) published their research on "Maximum entropy modeling of species geographic distribution". The method they suggest is very well suited to develop distribution models from presence only data. Without going into the mathematical detail of the computations of

Maxent it is useful to note that the maximum entropy approach by definition agrees with everything that is known but carefully avoids assuming anything that is not known (Jaynes, 1991). More technically expressed this means that a certain probability distribution maximizes entropy while subject to certain constraints representing our incomplete information. These constraints represent the fundamental property which justifies use of that distribution for inference. The method's origins lie in statistical mechanics (Jaynes, 1957), and can be attributed to the school of machine learning. Maximum entropy remains an active area of research with an annual conference (Maximum Entropy and Bayesian Methods) that explores applications in diverse areas such as astronomy, portfolio optimization, image reconstruction, statistical physics and signal processing (Phillips et al., 2006).

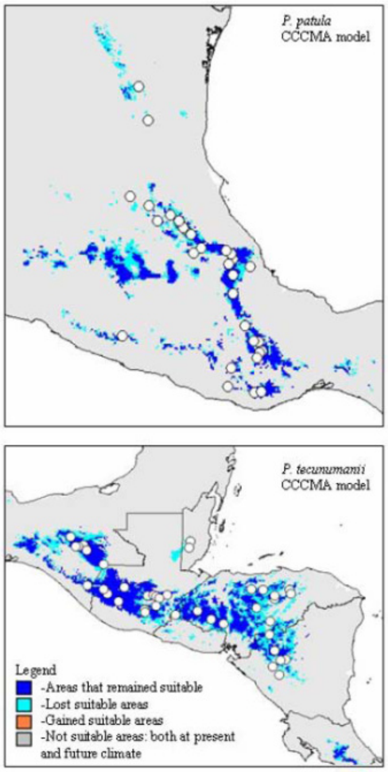


Fig. 3 Maxent's climate change impact prediction for the natural distribution of *Pinus patula* and *Pinus tecunumanii*.
Adapted from van Zonneveld et al., 2009

1.2.2. Model validation

The most common approach to validate predictions from CEMs separates the collection of geo-referenced species occurrence into a test- and a train dataset. Usually 80 % of the available data is used to run the climate envelope model (train data) and the remaining 20 % are used to evaluate the accuracy of the developed distribution model. This approach generally follows the demand in statistics that robust measures of prediction success make use of independent data that was not used to develop the model. The best way how to partition data is still discussed among researchers. Fielding and Bell (1997) state that the ecological research community seems to have paid little attention to how the partitioning method can influence the error rates. Only Verbyla & Litaitis (1989) reviewed a range of partitioning methods in their assessment of resampling methods for evaluating classification accuracy (Fielding & Bell, 1997). It is in general believed to be beneficial in order to make the accuracy estimate less dependent on one single partition to average results from several partitions. This results into the so called k-fold cross validation of species distribution models, where "k" stands for the times data was partitioned into a test and train dataset.

The standard method to assess the validity of predictive distribution models is the so called area under receiver operating characteristic (ROC) curve also simply known as area under curve (AUC). ROC and AUC are commonly used as measures of climate envelope model predictiveness (Fawcett, 2004) and yield a score between 0 and 1. This score has been shown to be equivalent to the probability that a model assigns a higher probability of occurrence to a location where the species actually occurs. An AUC score of 0.5 indicates poor model performance, equal to random predictions of the so called "null model". A score of 0.9 or above indicates excellent model performance (Araújo, Pearson, Thuiller, & Erhard, 2005). The AUC validation technique is subject to much criticism and remains an active field of research.

1.2.3. Shortcoming of climate envelope models

Doorman (Dormann, 2007) and Thuiller (Thuiller et al., 2008) reviewed the current state of science of ecological niche modeling and took a critical look at the limits and shortcomings of global change projections of species distributions. One major limitation of these models is considered to be that important evolutionary processes are often overlooked when evaluating future species distribution. The vast majority of modeling approaches do not take into account that a species' climatic envelope is not consistent and that changes could alter the environmental niche considerably (Dormann, 2007; Kremer et al., 2007). This often results in an overestimation of climate change's impact and puts studies as a basis for decision making to question.

Another aspect that makes climate envelope models underestimate a species possible distribution is related to unsaturated habitats or species interaction (Fielding & Bell, 1997). The realized and fundamental niche of a species is often not congruent and CEMs making inferences from the one to the other often lead to erroneous predictions.

Researchers who aim to develop and apply bioclimatic models in an informative way require a deeper understanding of a wide range of methodologies, including the choice of modeling technique, model validation, statistical phenomena such as colinearity, autocorrelation, biased sampling of explanatory variables or scaling and impacts of non-climatic factors. Heikkinen, et al. (2006) state that the key challenge for future research in the field of CEM is integrating factors such as land cover, direct CO_2 effects, biotic interactions and dispersal mechanisms. Bioclimatic envelope models have a number of important advantages but they should only be applied when users of models have a thorough understanding of their limitations and uncertainties (Heikkinen et al., 2006).

A more general point of criticism raises Knight (2008) by elaboration on the Knowing-Doing Gap in conservation science as a whole. He states that given the woefully inadequate resources allocated for conservation, his findings raise questions over the utility of conservation assessment science, as currently practiced, to provide useful, pragmatic solutions to conservation planning problems. There is need to reevaluate the conceptual and operational basis of conservation planning research. He concludes with 7 concrete recommendation for actions to begin a process for bridging the research–implementation gap in conservation research (Knight et al., 2008).

For a more detailed discussion of criticism on CEM predictions the reader is referred to the comprehensible review "Promising the future? Global change projections of species distribution" (Dormann, 2007).

1.2.4. Correlative - combined with mechanistic models

A recent development aims to improve the quality of species distribution models (SDM) and climate change impact predictions studies by integrating predictions from fundamentally different modeling strategies. By combining correlative models (such as Maxent) with mechanistic models we try to capture a species physiology and make predictions on habitat and population parameters more robust and reliable. Kearney et al. (Kearney, Wintle, & Porter, 2010) demonstrated this approach on the current and future distribution and fertility of an Australian gliding possum. They used Maxent and another simple CEM, Bioclim, as correlative species distribution models and Niche Mapper as mechanistic model.

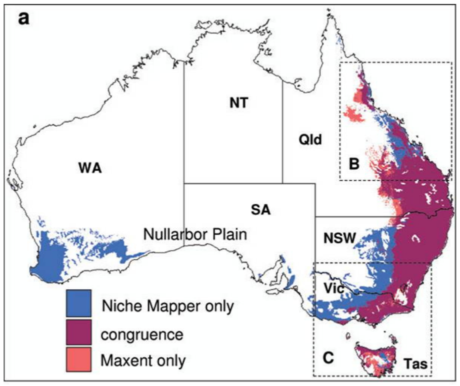


Fig. 4: Congruence between mechanistic – and correlative model.
Adapted from Kearney et al., 2010

The greater gliders that were modeled in this work are nocturnal specialist feeders on *Eucalyptus* leaves. With the help of Niche Mapper areas suitable for the species were modeled based on a number of different physiological responses to the environment (e.g. fur properties, core body temperature, digestive system and milk production). Their correlative SDMs approach used app. 6,000 recorded sightings. They based the distribution model on gridded layers of environmental data on mean annual temperature, mean precipitation of the wettest/driest period and categorical data of land cover a map of species' suitability. Kearney's et al. finding was that Maxent and Niche Mapper both yield qualitatively identical results (figure 4) suggesting that when temperature and species are main direct driving factors influencing a species distribution correlative SDM can yield reliable predictions.

Robertson, et al came to a similar conclusion in an earlier study (Robertson, Peter, Villet, & Ripley, 2003). Their results suggest that correlative models can perform as well as or better than simple mechanistic models. They draw the general conclusion that predictions generated from the different model designs are likely to generate different insights into the potential distribution and biology of the target organism and thus each approach may be appropriate in different situations (Robertson et al., 2003).

1.3. Forest growth models

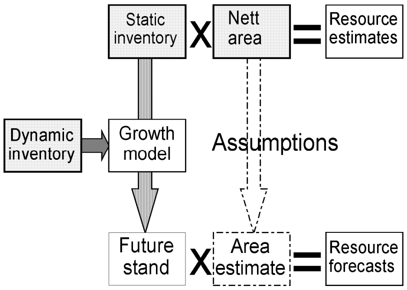


Fig. 5. The role of growth models and complementary data in providing decision support.
Adapted from Vanclay, 1994

The principle of sustainable forest management requires a profound understanding of the factors controlling tree growth and an understanding of the limitations of the sites on which trees are planted (Louw, 1999). This insight can only come from a large amount of information on parameters that influence growth dynamics and site preferences. Especially when the aim is the production of commercially valuable timber, it is important to estimate present growth or future growth potential (Subasinghe, 2011). For this purpose forest growth models offer an abstraction of the natural growth and stand dynamics. They enable us to give information on important parameters such as volume growth, mortality and changes in stand composition and structure. The models have proven to be very useful tools for research and management where they are mainly used for predictions of future yields and for the exploration of different silvicultural management options (Vanclay, 1994). The models designed for research tend to be more demanding in terms of input data and rely on information that is usually not readily available for commercially managed forests. Models designed for management use simpler and more accessible data which can be obtained during common forest inventories. Figure 5 gives a schematic overview of the process how forest growth models can facilitate decisions in sustainable forest management by giving a realistic resource forecast.

The studies that form this cumulative PhD thesis deal with pure even-aged pine stands. The statistic modeling techniques we implemented therefore do not apply for forest stands with trees of many ages or many species. For possible solutions towards the realistic estimation of growth and stand dynamics in mixed forests the reader is referred to Vanclay's comprehensive work on "Modeling forest growth and yield: applications to mixed tropical forests" (Vanclay, 1994).

1.3.1. Statistical models vs process based models

The three studies discussed in this report make use of statistical, correlative techniques to predict suitability of species occurrence or as in the later two studies, to predict height growth under different environmental conditions. These correlative techniques are very helpful when there is no, or not sufficient data on the studied species' physiology available. Process based models which rely on this physiological data are next to correlative approaches the second important school of forest growth models. These process based models can be defined as mathematical representations of biological systems that incorporate our understanding of physiological and ecological mechanisms into predictive algorithms (Johnsen, Samuelson, Teskey, McNulty, & Fox, 2001).

There are many such models available and they are frequently used in yield predictions studies, which were still mainly undertaken in a research context (3PG, Yield-Safe, FinnFor, CABALA, Formix 3-Q to name only a few). Louw expects that the simulation of ecological processes influencing tree growth will, in future, receive preference over the use of discrete site variables to predict the growth of trees (Louw, 1999). Nevertheless, the prevalent perception remains that process based models are suited only for research applications and that management questions will be solved primarily by using descriptive empirical models (Battaglia & Sands, 1998). The reason for this impression lies mainly in the high demand process based models still have in terms of quality and quantity of input data.

Matala et al. in their “Comparison of a physiological model and a statistical model for prediction of growth and yield in boreal forests” (2003) assessed the structural and functional properties of a physiological model (FinnFor) and a statistical model (Motti). They analyzed these two different model concepts in order to ascertain whether a physiological process based model would provide the same prediction capacity as a statistical model, which is based on long-term inventory data. The three criteria used for comparison were (1) stand-level variables, (2) analysis of volume growth graphs, and (3) stand structure variables. The study comprised data for *Pinus sylvestris*, *Picea abies* and *Betula pendula* all growing on medium-fertile sites in central Finland. Matala et al. found that in general, the outputs of the models agreed well in terms of relative growth rates regardless of tree species, with the implication that both models predicted competition within a stand and the effect of position on tree growth in a similar way. The statistical model was stable in its predictions, but not as sensitive to initial stand conditions as that based on physiological processes. Nevertheless it can be said that the two models agreed well in their dynamics and predictions. This lead Matala to recommend that some elements of process-model thinking could be incorporated into statistical models in order to make these responsive to changing conditions (Matala et al., 2003).

Where detailed data from growth inventories are available statistical models can be used but especially where the effect of different management options is to be analyzed, process based models react more sensitively to changes in input parameters. Mechanistic models can be used to evaluate the impacts of thinning on mixed species stands for example and multiple silvicultural regimes can be assessed without expensive and time-consuming field trials (Bartelink, 2000). To benefit from the advantages of both model types so called hybrid models are developed. These models are a mix of process-based and correlative models and can avoid some of the shortcomings of both approaches. Hybrid models include a mechanistic description of the environmental influences into a statistical growth and yield model. Hybrid models provide an increase in biological realism over simple empirical growth models, yet do not require the level of parameterization of process-based models (Mäkelä et al., 2000).

For a brief discussion of the comparison of process based models and correlative models for the estimation of species distributions see also section 1.2.4.

1.3.2. Evaluation of forest growth models

An important part of any model building process is its evaluation in terms of how well it reflects the reality and how well does the model enable us to make realistic predictions and forecasts. Validation and verification are two important parts of this evaluation. The two step evaluation-process translates in forest growth modeling into qualitative (verification) and quantitative (validation) tests (Vanclay & Skovsgaard, 1997). Vanclay and Skovsgaard suggest the following framework to evaluate the quality of growth models: Examine (1) logic and biologic assumptions, (2) statistical properties, (3) characteristics of errors, (4) residuals of the model, and (5) conduct a sensitivity analyses.

Evaluation should not come as an afterthought to the model construction, but should be considered at every stage of model building; during its conception, its design and construction. Primarily evaluation bases on regression techniques (Vanclay & Skovsgaard, 1997). The quality demands on a model in terms of logic structure and from theoretical and biological views are the following: Assumptions should be parsimonious, biologically realistic, consistent with existing theories of forest growth, and the model should be able to predict sensible responses to management actions.

The site quality models we developed for “Adaptation of tropical and subtropical pine plantation forestry to climate change: Realignment of *Pinus patula* and *Pinus tecunumanii* genotypes to 2020 planting site climates“ (Leibing et al., 2009) and “Selection of Provenances to Adapt Tropical Pine Forestry to Climate Change on the Basis of Climate Analogs” (Leibing et al., 2013) do not meet all of the above mentioned criteria. The reason for this lies in the scope of these studies. Their target was not the realistic prediction of different silvicultural management regimes. Furthermore, we dealt with in terms of species and age homogeneous stands and not with heterogeneous natural forests. This made the prediction of growth potential less complicated and following the parsimonious criteria some of Vanclay and Skovsgaard's quality criteria for model evaluation could be neglected.

1.3.3. Challenges for practical implementation

The most basic approach towards modeling forest yield is to make inferences from a site's historic tree growth. Historic growth records build the basis for a site index which is thought to inform about future yield expectations. These traditional growth and yield models have the common disadvantage that they must assume a site index to remain constant and are therefore insensitive to changes in environmental, site or silvicultural conditions. This school of models might appear too simplistic and unrealistic but still today these are the principal yield models used in forest management (Johnsen et al., 2001).

There exist, as discussed earlier, the modern process based models that try to realistically reflect important parameters for tree growth such as rates of photosynthesis and stomatal conductance. They basically attempt to estimate carbon gain at the cellular level and model the carbon balance of leaves based on calculated microclimates within the canopy, canopy architecture, leaf area, leaf type (sun, shade) and the resource composition of various portions of the canopy (Johnsen et al., 2001). This already makes clear why many process based models are not suited for practical implementation. Simpler model versions that try to aggregate processes and by this reduce data demand might be more applicable in a forestry management context.

Already today growth cannot be reliably predicted from past performance. Eutrophication from industrial activities or climate change altered the abiotic environment in a way where future growth rates cannot be accurately predicted from site indices. One good example for this are the intensively managed southern pine plantations. By using competition control, fertilization, and superior genotypes, productivity increased in these stands threefold (Borders & Bailey, 2001).

A way out of the trap between static site index models and complex process based models offer site quality models that are not derived from past performance data but from biophysical climate and edaphic variables (Ung et al., 2001). The underlying assumption is that the relation between height and age of the dominant trees depends principally on a site's bioclimatic set-up (degree days, aridity index and precipitation) and edaphic properties (e.g. soil water holding capacity). Biophysical site index models based on this assumption enable us to consistently predict site potentials under diverse- and changing conditions. This school of models is the nearest equivalent to the height growth and site quality models we developed for *Pinus patula* and *Pinus tecunumanii* in the second (2.2) and third (2.3) study. I will present the approach and methodology of these studies in greater detail in the following paragraph.

2. The published manuscripts in context of the current research agenda

This chapter aims to put the publications which constitute the cumulative PhD thesis in context of the current research agenda. The first study (van Zonneveld et al., 2009) evaluates techniques that estimate the persistence of natural populations in the face of climate change. The second and third study (Leibing et al., 2013, 2009) focus on climate change effects on growth potentials in productive forest plantations. The underlying research question is how GxE can best be exploited by adapting the choice of seed material to future climate conditions.

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

Before the first study will be discussed I will give a brief and general overview over the expected impacts of climate change on natural tree stands.

One major threat climate change poses on natural forest stands, is the exacerbation of migration problems of marginal populations in fragmented landscapes (Mátyás et al., 2009). The unprecedented rate, at which the abiotic environment changes, will exceed the migration speed of many tree species and may therefore threaten the survival of valuable seed sources (Davis & Shaw, 2001). Climate change is further likely to alter species composition (Dukes & Mooney, 1999) and negatively affect plant-herbivore relationships (Coley, 1998). These alterations combined with anthropogenic pressure from habitat fragmentation, put natural population of many tree species at risk.

In this context the study "Climate change impact predictions on *Pinus patula* and *Pinus tecunumanii* populations in Mexico and Central America" aims to ascertain the impact of climate change on the persistence of the natural populations of the two closed-cone pine species at their natural locations. Possible negative impacts on populations should concern the forestry sector, as in the form of seeds, these are the source of genetic diversity used to sustain and improve plantation productivity under both present and future conditions (Dvorak et al., 2008). Natural stands of important plantation species hold the genetic variability needed to keep the species adaptable to new climatic conditions. Information is needed that helps to identify where most valuable genetic variations can be found and which seed sources will be under highest risk.

2.1.1. Objectives

The objective of the study was to evaluate the impact of climate change on the persistence of the natural populations of *P. patula* and *P. tecunumanii* species at their actual locations in order to inform about appropriate conservation actions. We aimed to (1) assess the adaptive ability of the two pine species based on the evaluations of provenance trials and (2) use the results of these field trials to validate CEM impact assessment studies on provenance collection sites in the wild.

2.1.2. Own contribution

The first step that laid the foundation for this study was the development of a work plan which formed the basis for collaboration between the three institutes: Bioversity International, CIAT and Camcore. I developed this work plan in May 2007 during my stay as visiting researcher at Bioversity International's Americas office in Cali, Colombia. This original plan was structured into three phases of which two were relevant for the studies summarized in this report:

Phase 1

- Determine bioclimatic profiles for the two pine species based on their natural ranges, supplemented with climatic data from localities where the species have been successfully tested as exotics.
- Use DIVA GIS tool and its climate envelope modeling tool Bioclim in order to identify appropriate planting/collection sites for *P. patula* and *P. tecunumanii*.
- Investigate the impact climatic change on the species natural distribution, using the CCM3 global circulation model.

Phase 2

- Determine the response (for wood volume production) of the two species and provenances to major climatic variables (average daily temperature, mean annual precipitation). Assess the extent of provenance x environment interaction.
- Identify options for selecting provenances with low provenance x environment and/or better adaptability to changed climates (higher temps, reduced precipitation).

- Assess the overall impact of two different climate scenarios on growth rates and productivity at sites where the two species are being commercially grown.

[…]

The work plan was approved by the three participating institutes in June 2007 and subsequently Camcore shared the provenance trial data for *P. patula* and *P. tecunumanii* with Bioversity and CIAT.

During my seven months stay at Bioversity International in 2007 I validated the province and trial location data following Hijman's suggestions (1999) and developed CEMs for the provenance location data. I noted that the models rarely predicted sites to be suitable where the species was proven to successfully grow if planted. I further elaborated on this finding by comparing climate ranges where the species exists in the wild with ranges where the species was planted. Provenance trials were clearly planted outside the climatic ranges where the pines grow naturally. The result of this simple comparison between ecological niches can be seen in figure 6.

I then applied the AUC technique to CEM results and found that this classic validation approach yielded excellent results for the niche model of *P. tecunumanii* and *P. patula*. But these high AUC scores well above 0.9 seemed to contradict the fact that trial growth and survival data indicated for both species stable growth rates outside the species' ecological niche. The CEMs did not seem to fulfill their purpose to realistically describe areas and climates where the species is able to grow. This finding led to the development of the translocational validation approach (see section 2.1.3).

I assisted Maarten van Zonneveld, German Lema and Andy Jarvis with the design of the appropriate methodology and selection of statistical techniques to test CEM results against provenance trial performance. We collaboratively conceptualized the methodology and addressed the comments of two peer-reviewers.

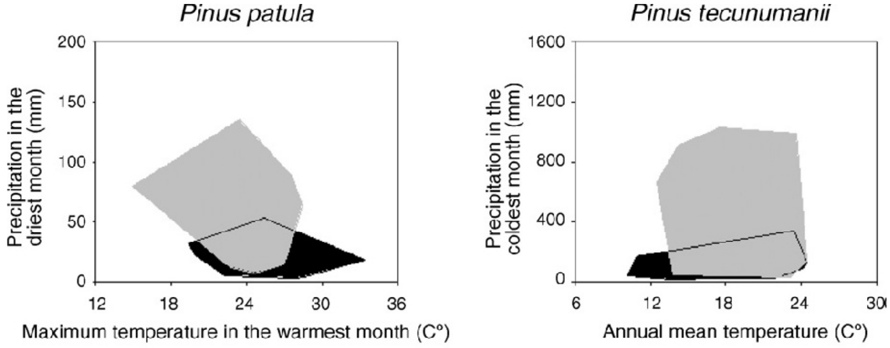


Fig. 6: Two dimensional linear combinations of variable range limits for natural pine habitat (in black) and the climatic ranges in which the field trials were established (in grey). Adapted from van Zonneveld et al., 2009

2.1.3. Methods

The following briefly section describes the methodology and statistical techniques we used for the study. First we validated the available provenance data. The dataset of Camcore seed collection sites consists of 24 *P. patula* provenances and 41 *P. tecunumanii* provenances. 7 points were added for *P. patula* from the Missouri Botanical Garden database.

The study area was defined by building a three degree buffer around the most northern, western, eastern and southern provenance location. All climate data was derived from a five km resolution WorldClim dataset (R. J. Hijmans, Cameron, Parra, Jones, & Jarvis, 2005) from which 19 BIOCLIM variables were calculated (Busby, 1991). In order to reduce the climate data's collinearity, we clustered correlated variables following the SAS VARCLUS procedure (Sarle, 1990). In order to identify meaningful climate variables, Mann-Whitney U-tests were conducted. We generated 500 random locations in a 300 km buffer around the provenance collection sites. Climate variables at these random locations with greatest difference from variables at provenance sites were chosen to enter the CEM calculation. If a cluster contained no variables significantly different from provenance locations, none were chosen.

The climate data for future conditions was extracted using Diva-GIS (R. Hijmans, Cruz, Rojas, & Guarino, 2001) from HADCM3, CCCMA climate model outputs for the year 2050 under the moderate emission scenario A2a (Solomon, 2007). The machine learning algorithm MAXENT was used to develop the CEM for current and 2050 climate conditions. We conducted a Chi-square test to find out if under future climate conditions the change in suitable area was significant. MAXENT's probability values at provenance locations were extracted using Diva-GIS and an AUC was calculated.

In the key part of this study, the translocational validation, we correlated CEM-generated suitability values for natural occurrence with observed height growth and survival at provenance trials which were established in a climate that matched with the climate at provenance locations. To identify sites with similar climates we calculated Euclidean Distances between provenance sites and field trials. As a threshold to define if a provenance site is a match to a trial site, 10 % of the smallest climate distances between natural provenances locations were used. If more than one trial was identified as a match the average height- and survival growth was calculated and used for the correlation.

To ascertain the natural and potential ranges of adaptive ability, two dimensional linear limits of variable ranges were developed. These simplified climatic envelopes compare climatic range at provenance locations to combinations of variable range limits at trial sites (figure 6).

2.1.4. Key findings

The key findings in terms of climate variable selection were that 5 climate parameters groups were clustered from the initial 19 climatic variables. The Mann-Whitney U-Test helped to effectively reduce the input variables that were fed into the CEM. It is important to note that this selection does not aim to identify important physiological factors that constrain the species' distribution. The aim was simply to identify a set of statistical meaningful climate variables that best describe the species distribution data.

In terms of AUC values the CEM for both species performed excellent. MAXENT runs with climate data derived from GCMs predict a significant decline in the number of suitable provenance collection sites for *P. patula* and *P. tecunumanii* (fig. 3).

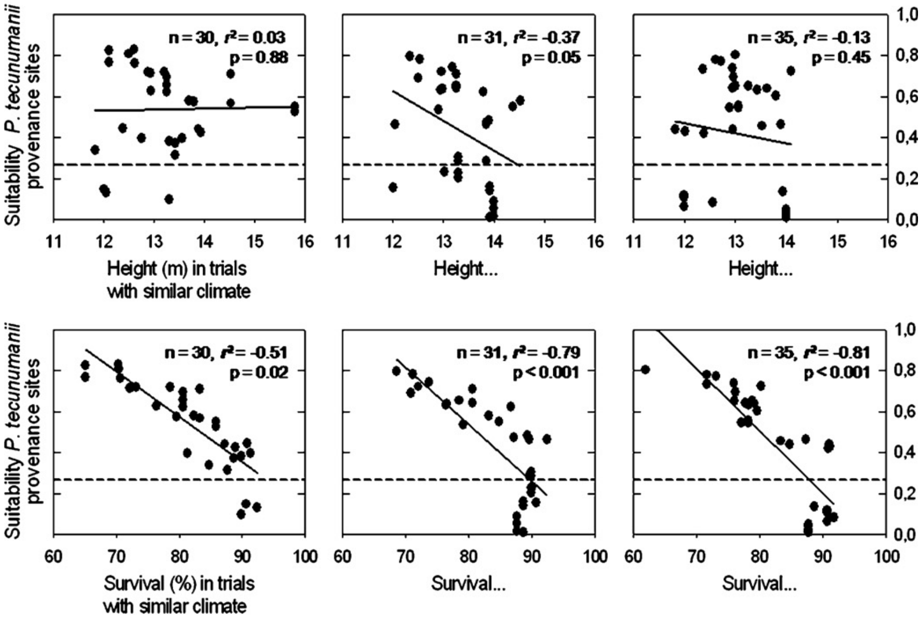


Fig. 7: Correlation of CEM-generated suitability values for *P. tecunumanii* provenance locations with height growth and survival rate on climatically similar sites where the species is grown as an exotic. Adapted from van Zonneveld et al., 2009

Interestingly enough CEM-assigned suitability values for natural pine occurrences did neither correlate positively with height nor with survival at climatically similar trial sites (figure 7). Both species appear to be adapted to a wider climatic niche than their natural distribution suggests.

2.1.5. Conclusion

The results clearly indicated that CEM results tend to underestimate the ability of pine provenances to thrive under climates they do not encounter within their natural distribution range. We have to denote however that in field trials where weeds are controlled and trees are planted as seedling, a species may perform well in a wider range of environmental conditions compared to its natural habitat. In a species' natural distribution range trees have to propagate via natural regeneration which may somehow limit their ecological niche. We are going to elaborate this point in greater detail in section "3.2.1 Performance in trials compared to survival in natural populations".

The data depicted in the scatter plots in figure **7** leave us confident to conclude that the investigated wild pine stands are likely to persist through substantial changes in climate. For the time being land use changes inside the species natural distribution range, urbanization, habitat fragmentation and livestock expansion appear to be more urgent threats to the species than climate change.

2.2. Adaptation of tropical and subtropical pine plantation forestry to climate change: Realignment of *Pinus patula* and *Pinus tecunumanii* genotypes to 2020 planting site climates

Not only natural tree habitat's but also planted forests are likely to be profoundly affected by altered precipitation and temperature regimes. More severe abiotic calamities such as cyclones with high peak wind speeds (Elsner, Kossin, & Jagger, 2008), wildfires (Wheaton, 2001) and droughts (Burke, Brown, & Christidis, 2006) are likely to threaten planted forests and put yield levels under pressure.

The International Tree Conservation & Domestication Program (Camcore), North Carolina State University, established large, multisite provenance trials. The data provide height and diameter growth for two *P. patula* varieties and two *P. tecunumanii* ecotypes. The measurements from these multisite provenance trials hold valuable information about seed choice for plantation establishment in time of rapid environmental changes. We developed a site quality model that statistically relates growth to environmental factors and couples the predictions to the average 2020 climate projections of four GCMs.

2.2.1. Objectives

The aim of this study was to test the suitability of seed material under changing climate of the two P. *patula* varieties *P. patula* var. *patula* and *P. patula* var. *longipedunculata* and *P. tecunumanii* highland- and lowland ecotype. Our objective was to (1) predict the impact of climate change on wood productivity for new rotation cycles that have an expected harvest time around 2025, and (2) identify the most suitable variety and ecotype of *P. patula* and *P. tecunumanii*, respectively, to optimize wood productivity under new rotation cycles.

2.2.2. Own contribution

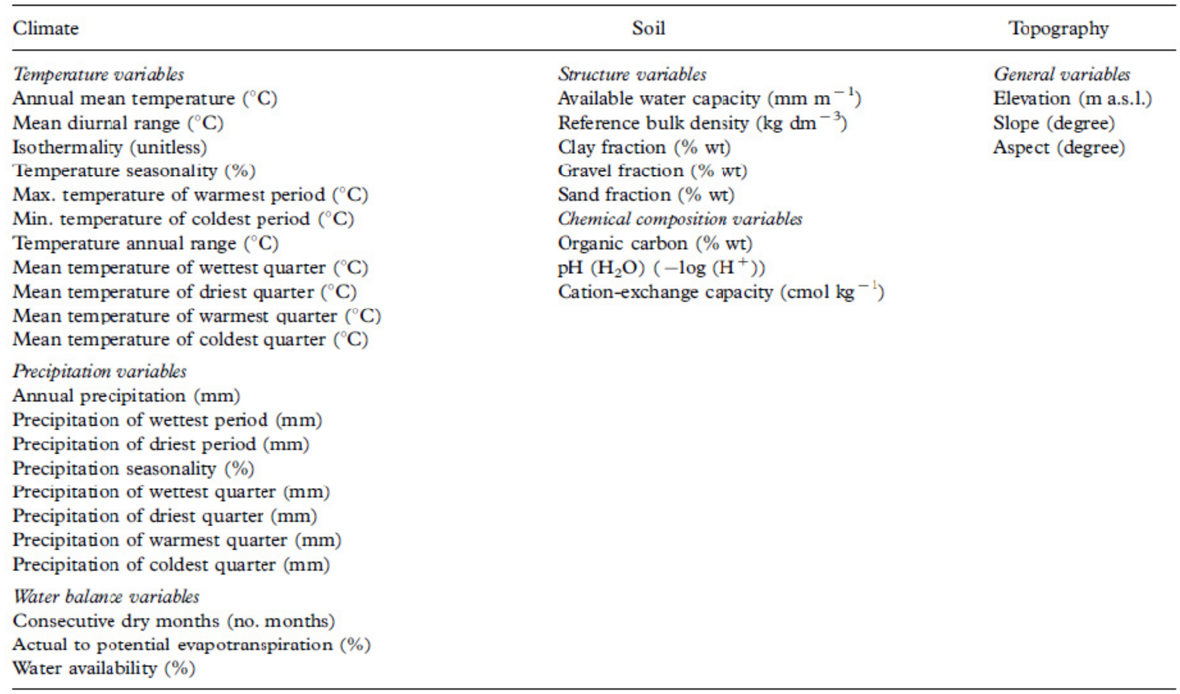
I conceptualized the study and principally developed the methodology. After a detailed literature research on climate change impacts studies and model building techniques I developed the idea to use centered squared value of environmental variables for the regression analysis. I presented the concept at the international seminar "Bosques Tropicales y Desarrollo" in December 2008 in Colombia, Medellin when first preliminary results were available. More mature results were later presented on the IARU International Scientific Congress on Climate Change, Copenhagen in preparation to the Conference Of Parties (COP 15) in 2009. In April 2009, assisted by my co-authors, I wrote the manuscript and submitted the original research article to the

"Scandinavian Journal of Forest Research". From May to November 2009 the article was in peer review. I improved the manuscript following the suggestions from two anonymous reviewers until the article was accepted for publication in December 2009.

2.2.3. Methods

The dataset for this study comprises 153 provenance trials which were established by Camcore between 1981 and 1997 in Colombia, Brazil and South-Africa (Dvorak, Donahue, & Vasquez, 1995). The validation of Camcore data showed errors in some of the geo-referencing. Site description did not match the information obtained following the suggestions from Hijmans, et al. (1999). These errors needed to be corrected since they could have seriously altered the results of the subsequent regression analyses. We extracted climate parameters, variables on water balance, and soil and topography data at trial locations using ArcGis. Data sources for the environmental data were WorldClim (R. J. Hijmans et al., 2005), for the Tropical Rainfall Measuring Mission (TRMM), the FAO Harmonized World Soil database (FAO & ISRIC, 2010) and digital elevation data (Jarvis, Reuter, Nelson, & Guevara, 2009). All variables, except those related to water balance from TRMM, were rescaled to raster data with a resolution of 30 arc-seconds. TRMM data was kept in its original resolution of 15 arc-minutes.

Tab. 1: List of environmental variables used to build the site growth models.
Adapted from Leibing et al., 2009



Climate	Soil	Topography
Temperature variables	*Structure variables*	*General variables*
Annual mean temperature (°C)	Available water capacity (mm m^{-1})	Elevation (m a.s.l.)
Mean diurnal range (°C)	Reference bulk density (kg dm^{-3})	Slope (degree)
Isothermality (unitless)	Clay fraction (% wt)	Aspect (degree)
Temperature seasonality (%)	Gravel fraction (% wt)	
Max. temperature of warmest period (°C)	Sand fraction (% wt)	
Min. temperature of coldest period (°C)	*Chemical composition variables*	
Temperature annual range (°C)	Organic carbon (% wt)	
Mean temperature of wettest quarter (°C)	pH (H_2O) ($-\log$ (H$^+$))	
Mean temperature of driest quarter (°C)	Cation-exchange capacity (cmol kg^{-1})	
Mean temperature of warmest quarter (°C)		
Mean temperature of coldest quarter (°C)		
Precipitation variables		
Annual precipitation (mm)		
Precipitation of wettest period (mm)		
Precipitation of driest period (mm)		
Precipitation seasonality (%)		
Precipitation of wettest quarter (mm)		
Precipitation of driest quarter (mm)		
Precipitation of warmest quarter (mm)		
Precipitation of coldest quarter (mm)		
Water balance variables		
Consecutive dry months (no. months)		
Actual to potential evapotranspiration (%)		
Water availability (%)		

The study was restricted to areas that have a similar bioclimatic set-up as the locations where trials were planted. The grid that was calculated to restrict the study area only contains locations where the 19 Bioclim variables (table 1) are in between maximum and minimum values of the values at trial sites.

In order to develop the site growth prediction models we built multiple linear regressions (MLR) models with centered normalized squared predictor variables. We used the forward stepwise regression method to identify statistically significant correlations between site growth and environmental variables. The linear regression models were cross-validated by setting 20 % of the data aside for model testing. The adjusted coefficient of determinations of the correlation (R^2) served as indicator for the quality of the model.

Based on the MLR models the ArcGis grid calculator was used to derive a spatial prediction of height growth. The equations used to derive the spatial predictions had the general form:

$$pht8 = b_0 + b_1 x_{i1} + b_2 x_{i2} + \cdots b_n x_{in} \; for \; i = 1,2, \dots n$$

where $pht8$ is predicted average height performance at age 8, b_0 is the intercept, b_1 is the Pearson's correlation coefficient with the dependant of first environmental variable, x_{i1} is the value of first environmental variable[...],b_n is Pearson's correlation coefficient with the dependant of nth environmental variable, and x_{in} is the value of nth environmental variable.

To calculate the climate change projection grids we used the outcomes of four GCMs and two emission scenarios. The GCMs available for this study were Canadian Centre for Climate Modeling and Analysis (CCCMA), Commonwealth Scientific & Industrial Research Organization (CSIRO), Hadley Centre Coupled Climate Model (HADCM) and National Institute for Environmental Studies (NIES). We calculated, based on the developed MLR models, height growth under current and future climate by 2020. Changes in performance for the best seed choice under current and future climate conditions were tested for their significance based on the results of a t-test. This approach showed where an adapted planting decision was predicted to bring significant improvement in height growth.

2.2.4. Key findings

Three of the four developed models were significant and robust. No reliable model could be developed for *P. patula* var. *longipedunculata*. Under current climate *P. tecunumanii* low elevation provenances are predicted to exhibit fastest growth in the majority of the study area. Overall climate change until 2020 is not changing height growth significantly. Nevertheless, in 7.3 % of the study area the current best seed changes under novel climate conditions of the year 2020.

This underlines two facts: (1) provenances are indeed adapted to their specific environmental conditions; and (2) it is important to conserve a wide range of seed sources to sustain the value of diversity for plantation forestry in heterogeneous environments and in face of changing site conditions.

2.2.5. Conclusion

Among others Spittlehouse suggests significant production losses if forestry does not adapt their management to climate change (e.g. D. Spittlehouse, 2008). The developed site quality models for two *P. tecunumanii* ecotypes and *P. patula* var. *patula* were statistically significant. Especially the goodness to fit ($R^2_{adj.}$) of the model for the *P. tecunumanii* lowland ecotype was excellent. Due to the ecotype's good survival and fast growth in warm and wet climates, these seed sources are likely to become more important in the near future.

Results of these and similar growth models based on geophysical site parameters may provide valuable decision support and help in the development of site-specific models for plantation forestry in general and pine plantations specifically.

2.3. Selection of provenances to adapt tropical pine forestry to climate change on the basis of climate analogs

2.3.1. Objectives

In the study "Selection of Provenances to Adapt Tropical Pine Forestry to Climate Change on the Basis of Climate Analogs" we assessed if the computation of climate dissimilarities can provide specific recommendations to adapt planted forests to climate change through a better use of forest genetic resources. By statistically relating trial's growth performance to climate dissimilarities between pairs of sites we aimed at identifying appropriate seed material of *P. patula* and *P. tecunumanii* in Colombia, Brazil and South Africa.

We compared two different approaches to measure climate dissimilarities and evaluated which approach correlates better with provenance height growth. In a second step we aimed to show that dissimilarity measures correlated with height growth can be used to identify well-adapted provenances to specific site conditions. This approach ideally demonstrates the potential and the restrictions in the application of climate analogues to support management plans with the aim to adapt existing and planned forest plantations.

2.3.2. Own contribution

As principal author of this study I developed the idea to use the climate analogue tool with the Camcore dataset. With the help of Maarten van Zonneveld and Andy Jarvis I conceptualized the methodology and ran the data intensive climate dissimilarity calculations on the workstations available in the DAPA centre in CIAT, Cali Colombia. After approximately two months of model runs I derived the results and drew technical conclusions together with my co-authors which led to the development of the original research article. The manuscript was submitted to the journal "Forests" in August 2012. In the subsequent months I lead the peer-review process and addressed the comments and suggestions of four anonymous reviewers. The article was accepted in February 2013 and published in March 2013.

2.3.3. Methods

As in the two studies before the data basis were the Camcore trials comprising growth data from 153 geo-references provenance trials. In order to break down the analysis from the species- or subspecies- to the provenance level we had to decide how many repetitions were sufficient to make a meaningful analysis of the relation between climate distances and differences in growth performance. We decided to only consider provenances that were planted in at least 6 different locations. Overall the number of repetitions on provenance level in the data chosen for the analysis ranged from 6 to 22. From the original 153 trials, 100 remained under this criterion and the selected data comprised height measurements of 10 different provenances.

The Analogue method we used to calculate climate dissimilarity was jointly developed by the Walker Institute at the University of Reading, CIAT and the Climate Impacts Group at the University of Leeds. The WorldClim climate data we used for the dissimilarity calculation had a resolution of 5- arc minutes. This equals a pixel size of approximately 85 km^2. For the impact analysis of climate change on provenance selection the results of an ensemble of 15 GCMs and three SRES emission scenarios was used. As in the previous study (cf. section 2.2) we restricted the study area by a simple climate envelope. Furthermore all protected areas were excluded from the study (figure 2).

We calculate dissimilarity values for each provenance and pixel inside the study area. The formula by which dissimilarity values between any pair of site were calculated reads

$$CCAFS\ Dissimilarity \ = \min_{o \leq lag \leq 11} \left(\sum_{m=1}^{m=12} \frac{DTR_m^f}{DTR_{(m-lag)}^p} \left(T_m^f - T_{(m-lag)}^p \right)^z + \left(P_m^f - P_{(m-lag)}^p \right)^z \right)^{\frac{1}{z}}$$

where DTR is diurnal temperature range, T is temperature, P is precipitation, m is month, p is present and f is future. The z parameter can be varied to perform a sensitivity analysis, but, in this study, the z parameter was kept constant at 2 to calculate standard Euclidean distances. We termed the calculated value "dissimilarity" and not "similarity" simply to follow the logic where a higher value of CCAFS climate dissimilarity indicates a pair of sites that is climatically more different from one another.

To assess if climate dissimilarity correlates to differences in height growth we use for each provenance the best performing site as a reference point and calculated for each provenance one dissimilarity grid. If our hypothesis is true, the differences in height performance relative to the best trial should show a significant correlation with the dissimilarity value for each of the inferior trials where the provenance was planted (figure 8). For clarification purposes let me give an example with the help of the scatter plot in figure 8. The point marked with

"A" indicates the trial with top height growth for which we calculated climate dissimilarities. The point marked "B" indicates a trial planted at a different locations but with seeds from the same provenance. This trial (B) exhibited 2.85 m less height growth as compared to trial (A) and is found at a location associated with a climate dissimilarity value of 137.

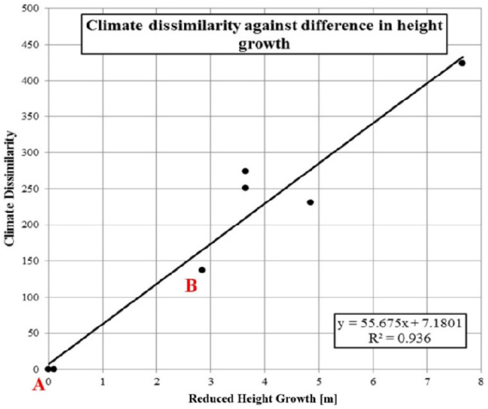


Fig. 8: Scatter plot showing the linear correlation of climate dissimilarity and height growth. Adapted from Leibing et al., 2013

2.3.4. Key findings

The example of the relation between climate distance and difference in height growth showed the data for *P. tecunumanii* provenance Campamento which originates from Honduras. For this seed source, climate dissimilarity values clearly correlated with differences in height growth. The coefficient of determination of the correlation equals 0.936. The more different climate becomes from the optimal growth conditions (A) the lower our achievable growth performances. But climate dissimilarity values were not always found to be a reliable indicator for growth rates. The Analogue method seemed to work well for the tested *P. tecunumanii* provenances but not for seed sources from *P. patula*. Or in other words climate dissimilarity calculations served as a useful tool to indicate site–provenance–climate relationships in *P. tecunumanii*. For *P. patula* we could not find any meaningful relationships. Analogue models yielded an average R^2 value of 0.68 for *P. tecunumanii* provenances and an average R^2 value of only 0.12 for *P. patula*

Concerning the modeled impact of climate change on yield levels analogue runs suggest that if foresters chose seed sources which are adapted to the novel climate conditions, no yields reduction have to be expected. Compared to plantation areas in South Africa and Brazil, Colombia is predicted to have the highest yield potentials under current and future climate conditions. At the same time in Colombia the study area's heterogeneity in terms of modeled height growth is highest. The model runs showed that planting sites in Colombia are most sensitive to the choice of climatically well-matched seed material.

Table 2 indicates in which percentage of the study area individual provenances were modeled to exhibit best height growth**.** Under current climate, the *P. tecunumanii* high elevation provenance Chempil is predicted to be the best choice in terms of growth performance in 65.9% of the study area. In the Colombian states of Valle del Cauca, Santander and Huila, the seeds from the provenance Campamento yield the highest growths rates. Also when planted in southern Brazil, in the state of Rio Grande do Sul, Campamento was found to be the best seed choice. Close to the coast, in the low land of the two Brazilian states Espirito Santo and Rio de Janeiro, *P. tecunumanii* low elevation provenances Jocón and San Jeronimo show most promising growth rates.

Tab. 2: Percent of study area where the respective provenance is expected to be best seed choices under current and future climate conditions. Adapted from Leibing et al., 2013

	Current Climate			Change by 2030			Change by 2050		
Provenance	**Colombia**	**Brazil**	**South Africa**	**Colombia**	**Brazil**	**South Africa**	**Colombia**	**Brazil**	**South Africa**
Jocon	1.94	6.96	0.07	-1.19	-0.89	-	-1.38	-0.67	-
Campamento	21.07	14.02	0.04	1.00	2.31	-	2.19	4.02	-
Chempil	74.61	69.08	58.23	0.16	-0.74	-2.23	-1.50	-2.16	-9.63
San Jeronimo	1.57	7.41	10.50	-0.66	-0.01	3.08	-0.60	-0.62	4.45
Huay	-	-	-	-	-	-	-	-	-
Chanal	0.82	2.54	31.16	0.69	-0.67	-0.74	1.29	-0.58	5.29

2.3.5. Conclusion

Climate dissimilarity correlated with differences in height growth allowed us to distinguish between seed sources that have good height growth in a specific climate, like most *P. tecunumanii* provenances, and provenances that have a more moderate height growth but that adapt well to a wide climate range, such as most tested *P. patula* provenances. Climate similarity calculations like the analogue method used in this study may be particularly useful to identify suitable areas for the climate specific *P. tecunumanii* provenances. But in the light of a rapidly changing environment the finding that *P. patula* provenances appear to be rather indifferent to changes in climate may be of even greater importance. In the face of great climate uncertainty, and today's shortcomings of climate models, it appears advisable to select species and provenances that are not overly sensitive to climate change.

3. Synthesis

In light of the increasing importance of productive forest plantations for the world's wood demand (Carle & Holmgren, 2008) decision support is much needed on how to adapt the management of these ecosystem to the new challenges brought about by climate change. The choice of planting material has to be adapted to maintain yield levels and information is needed which seed sources show potentially valuable traits for future breeding and plantation projects.

The requirements we have on these seed sources are manifold. They must exhibit good productivity over a number of different environments, must be relatively easy to breed for improvement, must have good disease resistance in commercial plantations, and must produce a type of wood that is demanded by the market (Dvorak, 2012). The three studies presented in this report aim to assist in the search of valuable planting material. First, we evaluated climate envelope predictions for natural pine occurrences. Results of this study showed if CEM serve to reliably predict climate change impact on the pine species' distribution ranges and if so, where valuable genetic diversity of *P. patula* and *P. tecunumanii* is likely to be threatened by altered precipitation and temperature regimes (compare figure 1).

A great part of the expansion of plantation areas are projected to occur in the developing countries and under tropical climates (FAO, 2010). So the target of a successful forest management must not only be to maintain growth in existing plantations but management also needs to focus on suitable plantation areas for plantation area expansions. The site quality models we developed in the second- (section 2.2) and third study (section 2.3) aim to give information about viable planting option on the one hand and on the other hand mapped out plantation areas that are expected to exhibit good growth performance under future climates.

The studies presented here all base on provenance trial data for two pine species. The closed-cone pines *P. patula* and *P. tecunumanii* for which growth data was analyzed are planted on more than 1.3 million ha in the tropics and subtropics (Dvorak, Hodge, & Romero, 2001). Market demand for the long fiber pulp produced on the majority of this area will increase rapidly. Smurfit Kappa Colombia, Camcore member responsible for the provenance trials in Colombia, estimates that demand for pulp from pine plantation will grow twice as fast as demand for short fiber from *Eucalyptus spp*. plantations (Smurfit Kappa Colombia, personal communication July 21, 2010). This once more emphasizes the special importance of stable and high yielding pine seed sources and the need to identify suitable areas for plantation expansions under future climate conditions.

3.1. Implications of key findings

The most prominent finding of the three studies is that, in general, in order to be able to adapt commercial plantation forests to expected climate change, seed sources from natural stands with the right set of traits (drought resistance, tolerance against high temperatures etc.) have to be collected and conserved. This implies that provenances which exhibit valuable traits have to be identified in large scale-field trials. Provenances, populations and families of important plantation species need to be tested in a wide range of environments. In a subsequent analysis of GxE interactions seed sources with desirable traits for climate change adaptation plans can be identified and selected for tree conservation and breeding programs. Often valuable seed sources belong to populations that exist at the species' distribution margin. Unfortunately, it is in many cases these marginal populations that are under most pressure. As in the case with *P. tecunumanii*, the pine is already under threat in Central America and southern Mexico and is classified as vulnerable according to the criteria of IUCN (Hilton-Taylor & Mittermeier, 2000). Individual populations are even critically endangered (Dvorak et al., 2000). But the chief concerns is not only that there are many of the populations of *P. tecunumanii* being destroyed in Central America and Chiapas, but that it is nearly impossible to get research amounts of seed out of Mexico. Complex paper work and bureaucracy impede the necessary flow of genetic material. The dangers and corrupt structures related to active drug traffic in the region make the continued easy flow of genetic material between countries a thing of the past in Mexico (Dvorak, W. personal communication March 22, 2012). The flow of seed material across the borders in Central America is still working fine.

Results of CEM are frequently referred to in scientific literature to direct conservation efforts and identify seeds from provenances with valuable traits that grow at a species' margin (R. Hijmans & Graham, 2006; Thuiller et al., 2008). These sources and their resistance to unfavorable climates such as frequent droughts and or high temperatures are expected to be of great value for future plantation efforts. The findings of our study "Climate change impact predictions on *P. patula* and *P. tecunumanii* populations in Mexico and Central America" published in Forest Ecology and Management in 2009 shed a somewhat distinct light on the validity of CEM outcomes. The results of the CEM Maxent do not account for the true adaptive capacity of the studied pine species. In our translocational validation we show that Camcore provenance trials are growing well in climates that Maxent predicts to be unsuitable (fig. 7). This implies that conservation actions guided by the results of CEM may well lead to misdirected efforts. In order to enable an efficient adaptation of forest management to climate change, forest genetic- and ecology research has to be synthesized to better elucidate the requirements of stability and response of forest ecosystems (Mátyás, 2006). It is important to mention that results in this sense are not only valid for the two studied pine species. Results from provenance trials can serve as the basis for translocational validation of CEM outcomes for other important pine plantation species (e.g. *Pinus kesiya* and *Pinus radiata* or e.g. *Eucalyptus spp*). For these species the forestry industry and its research cooperatives established multisite international provenance trials and the translocational validation method provides a way to validate CEM outcomes. In this sense the statistical comparison of CEM results with field data from provenance trials can help us to directly assess the true adaptive capacity of a range of important forest plantation tree species.

The forestry sector urgently needs decision support for sustainable management under climate uncertainty (Lindner et al., 2010; D. L. Spittlehouse, 2005). The assessment of options for intensively managed forests in terms of regeneration, tending, harvesting, protection, conservation and planning is no easy task. The results of "Adaptation of tropical and subtropical pine plantation forestry to climate change: Realignment of *Pinus patula* and *Pinus tecunumanii* genotypes to 2020 planting site climates" and "Selection of Provenances to Adapt Tropical Pine Forestry to Climate Change on the Basis of Climate Analogs" aim to facilitate a part of a decision model for managing forests under rapid environmental change. In view of expected climate instability, adaptability of forest trees causes serious concern due to the trees' long lifespan compared to the rapidity of expected changes in environmental conditions (Davis & Shaw, 2001; Mátyás, 2006). Our analogue method enabled the distinction between species and provenances with a fast growth but a narrow climate niche and those that are more "generalist". When selecting a seed source for planting in the context of climate change a forester's choice may very well turn in favor of a lower yielding but more reliable source. This way climate analogues could be a very valuable tool for foresters, not only helping to locate areas of highest suitability for a timber species with desirable characteristics, but identify what kind of tree should be planted now that will be resilient to climate changes 10 or 20 years in the future.

I would like to stress that findings from the three studies which constitute this cumulative PhD thesis could only be derived thanks to results from the homogenous growth trials established by Camcore members. This fact emphasizes the strategic importance of applied tree conservation programs and provenance trials to the forest industry. In a time where rapid environmental changes are eminent these programs are indispensable and provide a golden opportunity to get to grips with the adaptation processes of important plantation species to climate change.

There has, however, been a general decline in the establishment of provenance trials in recent years for a variety of reasons, including increased difficulty in international germplasm transfer (Koskela et al., 2007), their cost to maintain and measure, greater emphasis on social issues in the forestry sector and more attention to new technologies such as molecular marker analysis of genetic variation. Loo et al. (2011) nevertheless emphasize in their report on the state of knowledge of climate change and forest genetic resources that these molecular marker analysis should be seen as complementary to field trials and not as an alternative.

3.2. Critical remarks and model shortcomings

Even though we developed the methodology with great care and best available knowledge we cannot avoid that the models suffer from a number of shortcomings. The points of criticism I will summarize in this section do not question the validity of the previous discussed results or conclusions but aim to put the outputs somewhat into perspective.

3.2.1. Performance in trials compared to survival in natural populations

An important point of criticism to the study "Climate change impact predictions on *Pinus patula* and *Pinus tecunumanii* populations in Mexico and Central America" that is worth to be discusses is if we can say that a certain performance in trials is comparable to survival in natural populations. It can be argued that we mix up two different aspects when we look at areas where a species can compete and survive in the wild, and areas where it can be commercially produced. We show that the species are economically viable in environments that are different from the areas where it grows. That might be interesting albeit unsurprising if we look at common English gardens for example. Or we might think of any major crop; they have all moved outside their areas of origin into new environments. Thus an important research question that follows from this is why do the wild stands of the species not fill the "commercial niche"? Is it because that niche space is simply not available in the geographic range? Or is it because the species are out-competed by other species (or other land use)? The answer to this question has important implications for our analysis of the species' capacity to withstand climate change. In the first case, our conclusions remain reasonable, in principle. In the second case they do not make much sense, because the species will be competed out of the environments that they are not in now. If an in-depth analysis of this issue points towards the latter, this would severely undermine our thesis. This important point was not discussed in much detail in the published manuscript. A subsequent analysis of the niche space where the species performed well in trials has shown that this space is not available anywhere close to the pines' natural locations. Our argument that *P. patula* and *P. tecunumanii* exhibit sufficient plasticity to withstand medium term climate change at their actual locations remains valid.

3.2.2. The effect of extreme weather events

Another point of criticism is that we omitted the effect of biotic and abiotic calamities in our site quality models. The alteration of frequency and severeness of forest disturbances can have great impact on planted forests and the optimal planting decision. Some of the changes of the climate system show a large inherent variability and make it difficult to attach high levels of confidence to weather phenomena, particularly those associated with extreme events and/or where climate exhibits large natural variability (Hulme, 2005). Their influence on forest growth could not be assessed in the papers that constitute this cumulative PhD thesis since these extreme events are very difficult to model. For a comprehensive review of the likely effects of climate related disturbances on forests, the reader is referred to Dale's paper "Climate Change and Forest Disturbances" (Dale et al., 2001).

3.2.3. Environmental space covered by provenance trials

One key finding of the study "Selection of Provenances to Adapt Tropical Pine Forestry to Climate Change on the Basis of Climate Analogs" was that *P. patula* reacted insensitive to a range of different climates. We proposed that this makes the species especially valuable in a changing climate of uncertain direction and magnitude.

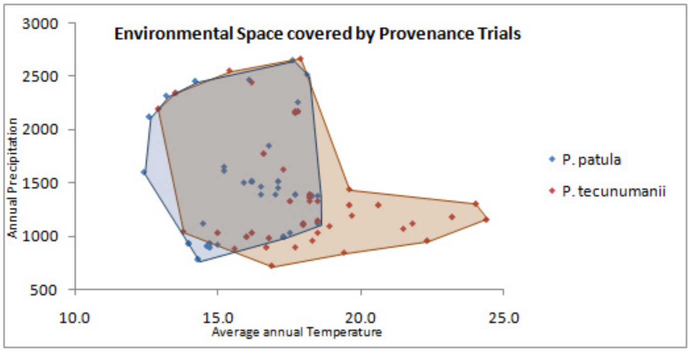


Fig. 9: Climate range covered by *P. patula* and *P. tecunumanii* trials.

It can be argued that the more stable response of *P. patula* could be also somewhat attributed to the fact that trials were placed in areas where *P. patula* plantations already existed and were known to grow well while *P. tecunumanii* was placed over a much broader area since Camcore and its members did exactly not know where it would do best. Figure 9 shows that 13 *P. tecunumanii* trials were planted in warmer climates, well outside the climate range occupied by *P. patula* trials. It stands to reason that if *P. patula* provenances would be planted in this broad climate range, Analogue would have less trouble to identify meaningful relationships between climate distances and growth performance. The implication this incongruence has on the findings was not analyzed in the published study. Nevertheless a subsequent examination of the data showed that if we omit *P. tecunumanii* trials that did not match the climate range of *P. patula* trials, growth responses are still stronger related to climate dissimilarities in *P. tecunumanii* than in *P. patula*.

3.3. Future research questions

The report concludes with a discussion of future research topics and work areas that enable us to reach an improved understanding of forest trees' adaptive capacity to climate change. In the following a list of research topics and management approaches will be given that could help foresters to successfully manage their stands in a time of uncertainty when climate changes in an unprecedented rate.

- Trials on species' ecological margins

Even for commercially important species where large multi site provenance tests have been undertaken, range margins and atypical populations that may be crucial for climate change responses are rarely well represented. There is, therefore, a lack of information on which to base proper tree–site matching for plantation planning

(Loo et al., 2011). Trials tend to be established in environments where a certain species is already known to grow well. Bio-physical site quality models would benefit greatly from trials in environments that represent the margin of a species' true fundamental niche. At these locations the species needs to exploits its full phenotypic plasticity and for a researcher the genotype's capacity to adapt to different climates becomes quantifiable.

- Change the seed source or create an adapted land race?

An interesting point was raised by Professor William Dvorak who is not only co-author for all three studies but also Director of the International Tree Breeding and Conservation Program. He asks to consider and evaluate two different strategies that would both lead to an improved adaptation of forest plantations.

The first option takes a forester back to a species' natural stands to plant a different seed source when climate change occurs. A second option would be to select trees in a plantation where the climate is changing to create an adapted landrace for planting in the next generation. The fundamental point the second strategy touches is that trees are known to adapt to their climatic setting very quickly (Dvorak, W. personal communication October 2013). The methodologies we developed are only able to evaluate the effectiveness of the first option, where we rely on seed material from natural stands. Which one of the two options eventually yield the better results in terms of high and stable growth performance in planted forests, cannot be answered with the available data. The results of a study based on the question if one should change the seed source or rather create an adapted landrace would sure be of great practicable importance for the forestry sector.

- Closer collaboration between practitioners and research institutes

One problem that circumvents the implementation of research results into practice is the missing coordination between research institutes and the forestry industry. Research that has the aim to change behavior in the forestry sector should correspond to current needs for decision support of forest companies. This may seem self-explanatory but experience shows that many forest growth models are too far away from reality for practitioners. Chances are high that if companies play a participatory part in the process of model building, they are more willing to implement results in their forest management programs.

- Long term Free Air Caron Dioxide Enrichment (FACE) experiments

There are virtually no yield models available that account for direct CO_2 effects on forest growth. This is largely due to a lack of quantitative data on CO_2 fertilization effects on seedlings, young plants and adult trees. FACE experiments especially in the tropics would help researchers to gain knowledge on this important effect of anthropogenic climate change on forest growth. Only then direct CO_2 effects can be included in growth models that more realistically predict climate change impacts on forest ecosystems.

- Validation of site quality models

The statistical validation techniques we use for our site quality models are often not considered proof enough for the forestry industry to adopt results for their management plans. One way to increase the trust of the forestry sector into developed decision support tools would be a so called ground-proofing of results. Small trials could be established that introduce a seed source into a climate that it is expected to encounter in its natural ecological niche or on plantation sites in the future. Growth rates and survival of the trees at these locations would be valuable evidence of the tree species' true adaptive capacity.

- Accuracy of General Circulation Models (GCMs)

In order to base decisions and forest management on the outcomes of climate change impact studies the accuracy of GCMs need to be improved considerably. Particular shortcomings of the models that impede a direct implementation of results into forestry practice are models' inability to account for micro climates such as cold pockets or the occurrence of infrequent extreme events such as heat waves or severe cyclones.

- Ex-sito conservation for conservation of valuable seed material

Seeds sources that exhibit valuable traits for climate change adaption need to be conserved ex-sito if anthropogenic pressure threatens their survival in the wild. Particularly seeds with traits that facilitate the adaptation of plantation forestry to novel climate conditions and to new threats arising from increased pest and disease occurrences need to be planted in areas where their long-term viability can be ensured.

- Synthesis of ecology and genetics in climate change studies

Diverse soil conditions and nutritional limitations remain, for model approaches, the most difficult parameters in predicting growth responses (Johnsen et al., 2001). The trend has to be not to only rely on pure statistical analysis but to investigate mixed models that combine knowledge about physiological process with empirical data obtained by field trials.

- Hybrid of *P. patula* and *P. tecunumanii* to reduce pest pressure.

The recently observed renewed interest in conservation has been brought about by the increase of diseases and pests in forest plantations and the need to have alternate species available in case of problems (Dvorak, 2012). Special focus in terms of pine plantation forestry lies in the breeding of hybrids of *P. patula* and *P. tecunumanii*. Site quality modeling for these hybrids could bring to light relevant results for the forestry sector especially in South Africa where pest pressure on *P. patula* plantation is particularly high.

3.4. Conclusion

This cumulative PhD project covers two main pillars of research relevant for the tropical forestry sector (1) We analyzed climate change impacts on the persistence of natural pine species populations at their actual locations and (2) we identified future growth potentials of different seed sources and identified climatically suitable areas for commercial pine plantations in Colombia, Brazil and South-Africa. The statistical tools we used to assess these climate change impacts were CEM and biophysical site quality models. The methods developed in this study can be applied to other tree species for which large provenance by environment experiments exist and offer a way to better understand and assess climate change impacts on subtropical and tropical plantation tree species.

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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.

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

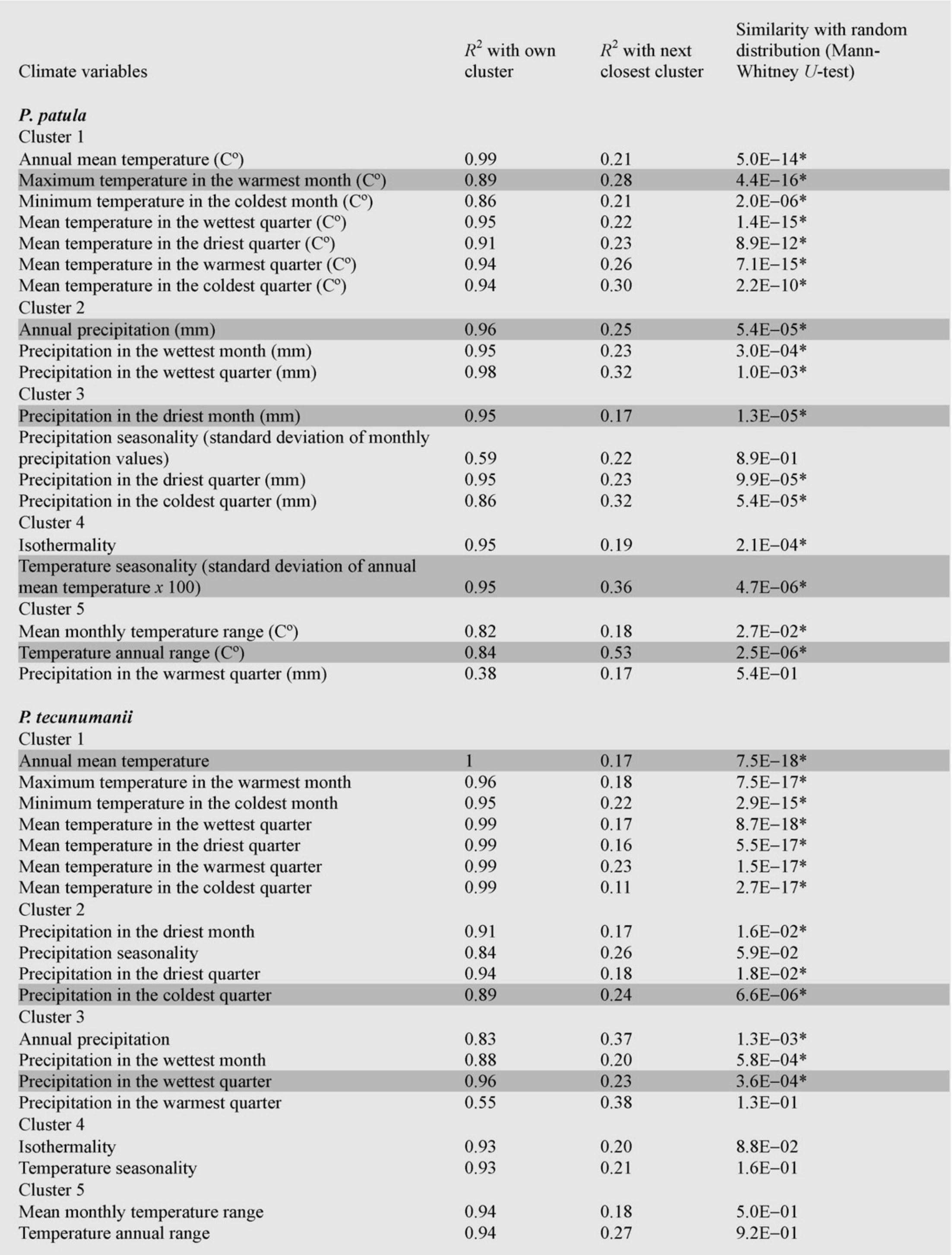
Validation points were identified for assessing the quality of the predictions in the climate envelope derived from Maxent. These validation points were acquired by correlating CEM-generated suitability values for natural pine occurrence with the observed height and survival at trials established in 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)
P. patula			
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 *x* 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
P. tecunumanii			
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.

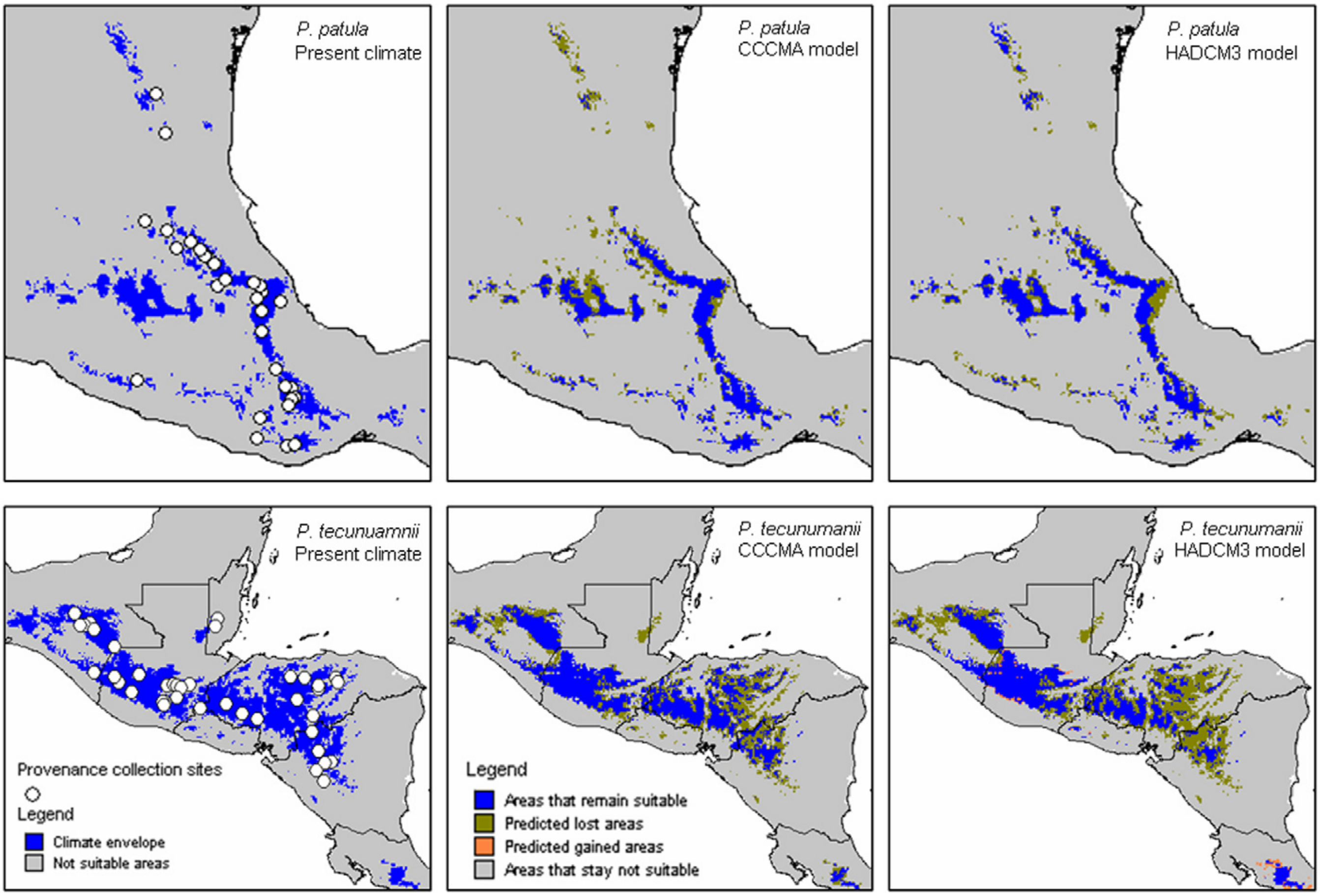


Fig. 1. Climate envelope maps for the natural distribution of *P. patula* and *P. tecunumanii* and the predicted impacts of climate change on their distribution by 2050, developed in the CEM modeling program Maxent. Areas were considered suitable for *P. patula* occurrence above a probability value of 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

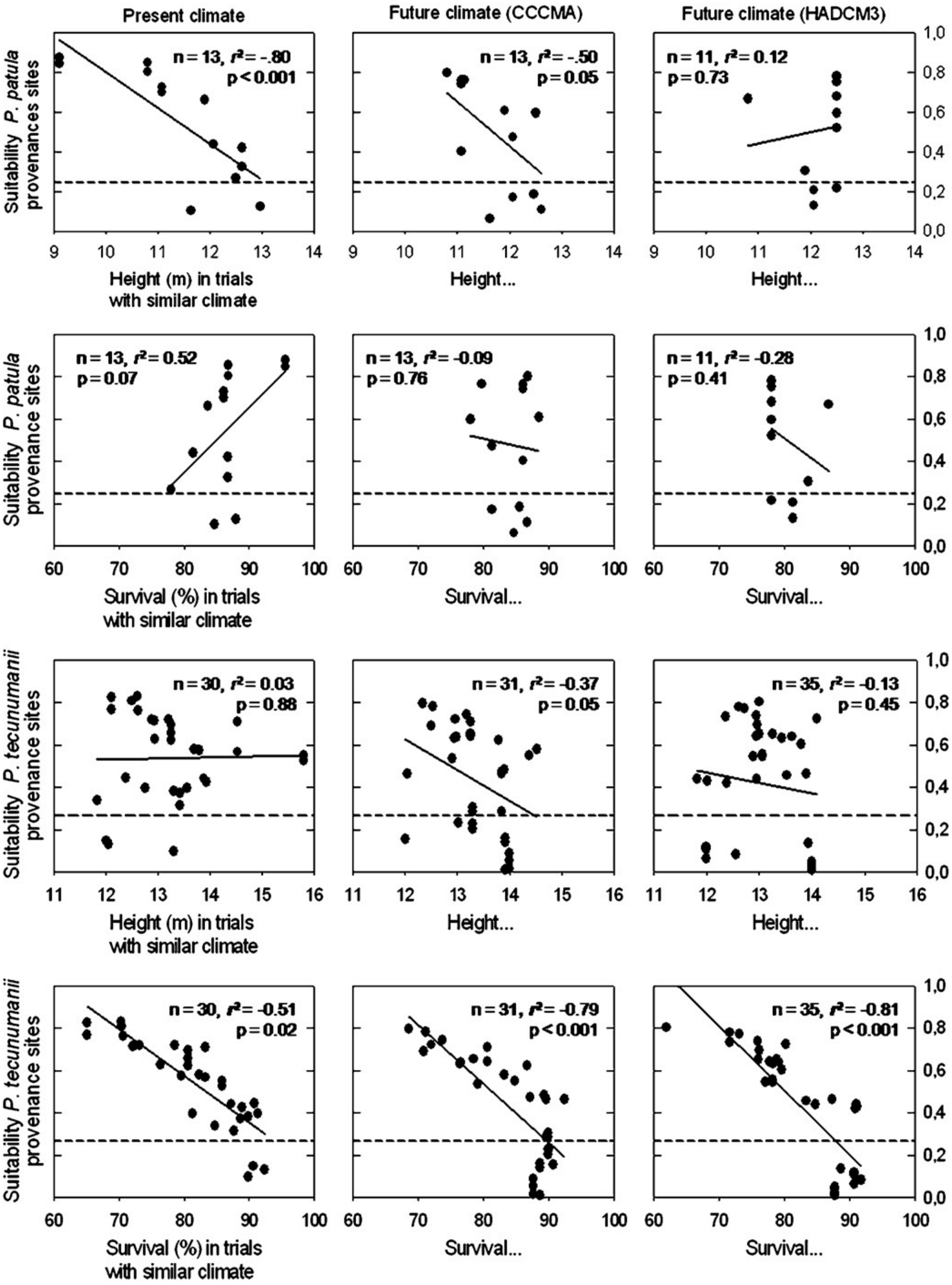


Fig. 2. Correlation of CEM-generated suitability values for natural pine occurrence with the observed height and survival at trials established in a present climate that matched respectively with the present climate and the predicted future climates at the provenance locations in the wild. A regression 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
P. patula			
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
P. tecunumanii			
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

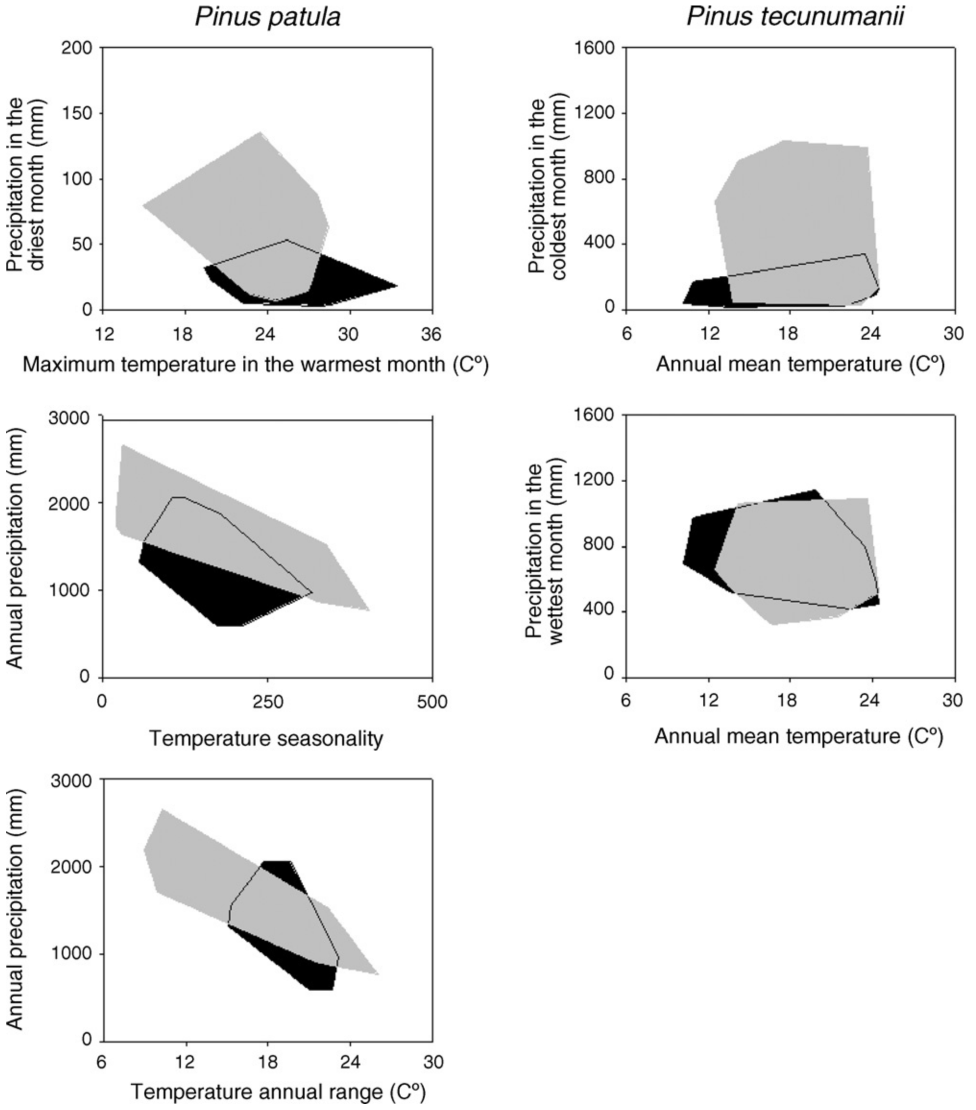


Fig. 3. Simplified climate envelopes for natural pine habitat (in black) and the climatic ranges in which the field trials were established (in grey), presented by two-dimensional linear combinations of variable range limits. Temperature seasonality: standard deviation of annual mean temperature × 100.

Table 3
Differences 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

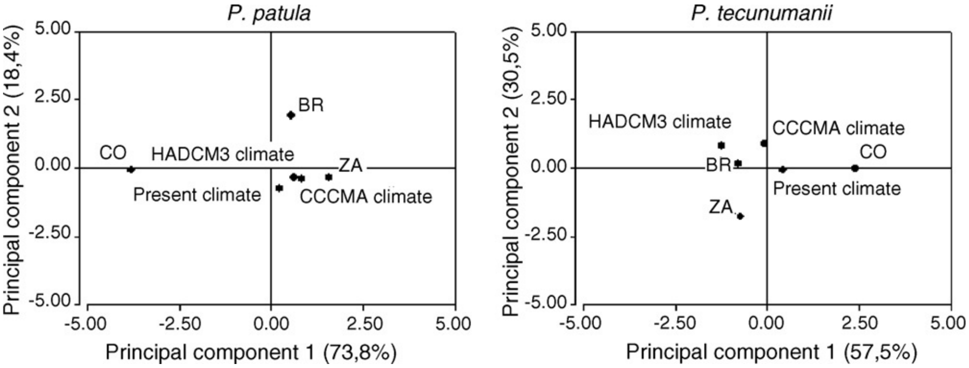


Fig. 4. Ordination with the help of principal component analyses (PCA) of average present climate and future climates (HADCM3 and CCCMA model) of provenance collection sites and the average present climate of field trials established in South Africa (ZA), Brazil (BR) and Colombia (CO) respectively.

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 trails. 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 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 *x* 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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ORIGINAL ARTICLE

Adaptation of tropical and subtropical pine plantation forestry to climate change: Realignment of *Pinus patula* and *Pinus tecunumanii* genotypes to 2020 planting site climates

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Abstract

Pinus patula and *Pinus tecunumanii*, two pines native to Mexico and Central America, are important plantation species for the forestry sector in the tropics and subtropics. In recent decades, members of the International Tree Conservation & Domestication Program (CAMCORE), North Carolina State University, have established large, multisite provenance trials for these pine species. The data provide valuable information about species and provenance choice for plantation establishment in many regions with different climates. However, since climate is changing rapidly, it may become increasingly difficult to choose the right species and provenance to plant. The aim of this study is to test the suitability of seed material under changing climate of two *P. patula* varieties (*P. patula* var. *patula* and *P. patula* var. *longipedunculata*) and two *P. tecunumanii* ecotypes (highland and lowland). For each variety and ecotype, a site quality model was developed that statistically relates growth to environmental factors and couples the predictions to the average 2020 climate prediction of four general circulation models. Three developed models were significant and robust. Provenances of *P. tecunumanii* from lowland areas in Central America are expected to be most productive in 2020 because of their promising performance under rather hot and wet climates.

Keywords: *Climate change impact predictions, height growth, management decision support tools, provenance trials, site quality modelling.*

Introduction

Global climate alterations are likely to affect the productivity of plantation forestry in the coming decades. Forest growth models suggest a substantial loss of production in the core area of current forestry if no appropriate action is taken (Fairbanks, 1999; Spittlehouse & Stewart, 2003; Savolainen et al., 2007). At the same time planted forests are becoming increasingly important to satisfy global wood demand (Carle & Holmgren, 2008). Planted forests may also indirectly reduce pressures in natural forests and are potential sources for carbon sequestration (Carle & Holmgren, 2008), and in that way contribute to the mitigation of climate change. To ensure the supply of the expected products and services from planted forests in the future under a changing climate, plantation forest management needs to be adapted accordingly (Kremer, 2007).

The selection of species and provenances that are most suitable to grow under the new climates that are expected to occur is an important aspect of a management plan that aims to adapt plantation forests (Spittlehouse & Stewart, 2003). It can be anticipated that seed material used in the past to establish new plantations will not be optimal under

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the changing climate in the future. New sources of seed will need to be found to optimize wood productivity.

In recent decades multisite provenance trials have been established to identify the most suitable species and provenances to plant in different climates (e.g. Dvorak et al., 1995; Hodge & Dvorak, 1999; Kanzler, 2002). Site growth modelling has proven to be a practical and accurate method to predict the performance of species and provenances in these experiments (Louw & Scholes, 2006). Support decision models that couple site growth modelling to future climate predictions based on general circulation models (GCMs) can be a useful tool for forest managers to choose which provenances and species to plant today in order to yield optimal growth during the rotations in future decades.

Significant areas of planted forests are grown in tropical and subtropical areas of Colombia, Brazil and South Africa (FAO, 2007). *Pinus patula* and *Pinus tecunumanii*, two pine species native to Mexico and Central America, are important plantation species for the forestry sector in the tropics and austral regions. Members of the International Tree conservation & Domestication Program (CAMCORE) have established multisite provenance trials on a global level that include 74 trials and 79 trials of *P. patula* and *P. tecunumanii*, respectively, to identify the growth and survival of these species and provenances across different environments. The results from these trials represent a treasure trove of data suitable for understanding how trees are adapted to their abiotic environment, and how they adapt to different conditions.

Pinus patula is one of the most important pine plantation species in tropical and subtropical regions, with close to 1 million ha established in plantations (Birks & Barnes, 1991). It is of primary importance in South Africa, where the pine is the most commonly planted species, accounting for 25% of the country's entire forest plantation area (FAO, 2007). Lesser amounts of *P. tecunumanii* are used in plantations, but it is an important plantation species in Colombia, and owing to its favourable growth characteristics and comparatively high resistance against pitch canker (Hodge & Dvorak, 2006) the species is also gaining importance in Brazil and southern Africa (Dvorak et al., 2000).

Pinus patula occurs naturally in the mountainous regions of eastern and southern Mexico. Two varieties can be distinguished: *P. patula* var. *patula*, which occurs in the eastern mountain ranges of the Sierra Madre Oriental, and *P. patula* var. *longipedunculata*, which occurs in the southern Mexican states of Guerrero and Oaxaca in the Sierra Madre del Sur (Dvorak et al., 2000). The geographical distribution of *P. patula* var. *longipedunculata* borders with the western distribution range of *P. tecunumanii.* The distribution of *P. tecunumanii* extends from Chiapas, Mexico, in the north to Honduras in the south and can be divided into two ecotypes based on altitude: a highland ecotype found in cloud forests at altitudes between 1500 and 2900 m, and a lowland ecotype that occurs at altitudes between 450 and 1500 m (Dvorak et al., 1989).

This study aims to contribute to the development of management plans to adapt existing planted forests in Colombia, Brazil and South Africa to the expected climate changes in the next few decades. It is hypothesized that in several areas, species and provenance choice of seed material will have to be changed in order to sustain the productivity of these planted forests. The objective of this study is to develop a decision support model that (1) predicts the impact of climate change on wood productivity for new rotation cycles that have an expected harvest time around 2025, and (2) identifies the most suitable variety and ecotype of *P. patula* and *P. tecunumanii*, respectively, to optimize wood productivity in the period of these new rotation cycles.

Materials and methods

To develop the decision support model, 8-year-old *P. patula* and *P. tecunumanii* height growth data were retrieved from a database of 153 provenance trials that were established by CAMCORE members in Colombia, Brazil and South Africa during 1981 and 1997 (Dvorak et al., 1995, 2001*b*). For each of the two *P. patula* varieties, *P. patula* var. *patula* and *P. patula* var. *longipedunculata*, and the two *P. tecunumanii* ecotypes, lowland and highland *P. tecunumanii*, three different site quality model types that examined relations between height growth and environmental conditions were developed. The models were cross-validated with an independent set of test data as an indication of model robustness. The model types that scored best in the cross-validation were used in the final growth prediction. Geographical Information Systems (GIS) were used to spatialize model predictions to other plantation areas and project them into the future. The average of four GCM climate projections for the year 2020 were used to calculate the expected impact of climate change on a plantation's growth performance in a time span that falls below the common rotation cycle of 17 years.

Study area

The study area comprises areas suitable for *P. patula* and *P. tecunumanii* plantations in current and future (2020) climates in Colombia, Brazil and South Africa. The areas include a topographic range from 25 to 2850 m of altitude and diverse climates that range from tropical conditions in the Colombian highlands, where annual rainfall frequently exceeds 3000 mm, to the dry, subtropical conditions characterized by cold and dry winters in South Africa, where the maximum annual mean temperature exceeds 20°C but temperature seasonality is more than 10 times as high as in Colombia. In South Africa in the coldest quarter of the year the temperature drops below 1°C. The trials were planted in parts of the northern tropical Andes in Colombia, and in southern Brazil, where trials are established in the states of Minas Gerais, Epirito Santo, Paraná and Santa Catarina. Trial sites in South Africa are located in the country's eastern escarpment from the Eastern Cape Province to the Northern Province. Management (site preparation, spacing of trees, weed control, etc.) among trials was as similar as practical in the field.

Data

The aim was to predict average observed height growth at the age of 8 years and select through stepwise regression the environmental variables that best explain height performance at trial sites. The pool of variables that were used as input consisted of grid-based climate, soil and topographical variables (Table I). Data for the 153 provenance trial locations were extracted using ArcInfo (ESRI, 2006). The 19 Bioclim candidate variables (Busby, 1991) were chosen to describe the climate in the study area. The data were derived from the WorldClim database developed by Hijmans et al. (2005). In addition, two water balance variables, water availability and potential to actual evapotranspiration, were calculated using satellite-based observation of rainfall from the Tropical Rainfall Measurement Mission (TRMM). Soil conditions (topsoil) were described by variables of the Harmonized World Soil database (FAO, 2009). Topographical variables were derived from the Shuttle Radar Topography Mission 90m Digital Elevation Data (Jarvis et al., 2008). All variable grids were scaled to the same spatial resolution of 30 arc-seconds, except for the TRMM-based variables, which have a resolution of 15 arc-minutes.

Model selection

Single regression analyses showed that some environmental variables predicted height growth best following a linear relation, while others did so

Table I. List of climatic, edaphic and topographic variables that were incorporated in the data table for the stepwise regression runs.

Climate	Soil	Topography
Temperature variables	*Structure variables*	*General variables*
Annual mean temperature (°C)	Available water capacity (mm m^{-1})	Elevation (m a.s.l.)
Mean diurnal range (°C)	Reference bulk density (kg dm^{-3})	Slope (degree)
Isothermality (unitless)	Clay fraction (% wt)	Aspect (degree)
Temperature seasonality (%)	Gravel fraction (% wt)	
Max. temperature of warmest period (°C)	Sand fraction (% wt)	
Min. temperature of coldest period (°C)	*Chemical composition variables*	
Temperature annual range (°C)	Organic carbon (% wt)	
Mean temperature of wettest quarter (°C)	pH (H_2O) ($-\log(H^+)$)	
Mean temperature of driest quarter (°C)	Cation-exchange capacity (cmol kg^{-1})	
Mean temperature of warmest quarter (°C)		
Mean temperature of coldest quarter (°C)		
Precipitation variables		
Annual precipitation (mm)		
Precipitation of wettest period (mm)		
Precipitation of driest period (mm)		
Precipitation seasonality (%)		
Precipitation of wettest quarter (mm)		
Precipitation of driest quarter (mm)		
Precipitation of warmest quarter (mm)		
Precipitation of coldest quarter (mm)		
Water balance variables		
Consecutive dry months (no. months)		
Actual to potential evapotranspiration (%)		
Water availability (%)		

Note: The table lists the environmental variables that were used to build the site growth prediction models.

through a quadratic relation (data not presented). Since it was not known beforehand which type of relations would weigh more in a multiple linear regression (MLR) model, three different types of MLR models were compared, all three using stepwise regression for the selection of model variables. The first model type, "Linear", consisted of standard linear relations between height growth and environmental variables. The second model type, "Squared", consisted of linear relations with centred-squared variables. In the third model type, "Mixed", the environmental predictors were either linear or centred-squared, depending on which type of relation explained best height growth in a single regression analysis. The development of squared centred variables is a recommended method to improve linear regression models (Bedrick, 2000). The value of the original environmental variable is centred by subtracting the variable's mean from each value and then squared. The transformed variables are then again related linearly to the dependent variable. Figure 1 exemplifies this variable transformation by showing the *P. tecunumanii* high-elevation population height growth linear, centred quadratic and centred-squared linear response to the annual mean temperature at the trial sites.

For each variety and ecotype, cross-validation of all three model types was carried out as an indicator of how the model could be extrapolated to larger areas. After Hurvich and Tsai (1990), 20% of the initial data set was used to validate the model types developed using the remaining 80% of data. As an indicator of robustness the coefficient of determination (R^2) was calculated based on the comparison between observed and predicted height of the test data. For each of the two *P. patula* varieties and the two *P. tecunumanii* ecotypes, the model type that scored best in the cross-validation was selected to perform the definitive growth prediction of the respective variety and ecotype, using all data.

Variable selection

To find the subset of predictors that best explain height growth, the stepwise regression algorithm was used. This is a common method in variable selection for site growth models (Huston, 1980; Dise & Wright, 2000). The stepwise algorithm defines the best possible set of variables to explain the variability in height growth at the age of 8 years. As variables are added during the model run there is continuous reappraisal of the existing set of included variables. If, in the light of the most recently added variable, an included variable no longer satisfies the retention criteria, it is deleted from the model (MacNally, 2000). The retention criterion of variables in the model runs was set on a probability value (p) of below 0.05. The coefficient of determination (R^2) was used to express the model's fit.

Multicollinearity among the explanatory variables (Xs) means that causal Xs may be lost from ultimate models because other, non-causal Xs are correlated with those causal variables and may be retained in models at their expense. To guard against the negative effect that multicollinearity has on the stability of regression coefficients and significance levels (MacNally, 2000), variance inflation (Vif) was calculated to indicate the rate of multicollinearity.

Variables were taken out of the modelling process if their Vif score exceeded 30, which is a common threshold to test for multicollinearity (O'Brien, 2007).

Model spatialization

To identify suitable seed material for plantation sites, Arcmap's grid calculator (ESRI, 2006) was used to project spatially the developed multiple linear regression equation for each variety and ecotype. Height growth of the respective variety and ecotypes is calculated for each grid in the study area based on the values of the environmental variables in those grids. The equations have the general form:

$$\text{pht8} = \beta_0 + \beta_1 x_{i1} + \beta_2 x_{i2} + \cdots \beta_n x_{in} \text{ for } i = 1, 2, \cdots n$$

where pht8 = predicted average height performance at age 8, β_0 = intercept, β_1 = Pearson's correlation coefficient with the dependant of first environmental variable, x_{i1} = value of first environmental variable [...], β_n = Pearson's correlation coefficient with the dependant of nth environmental variable, and x_{in} = value of nth environmental variable.

Current and future climate projections

The study area for which the site growth prediction models were developed was restricted to the environments that resemble the actual environmental niche in which the provenance trials are established. This avoids an extrapolation of the regression functions to environments where no empirical information was available and impedes the prediction of unrealistic and impossible height growths. A mask grid was calculated that comprises only the study area that has a similar bioclimatic set-up to the climatic niche in which the trials were established. The mask used the minimum and maximum values of the 19 BIOCLIM variables at the trial sites. All model operations use this mask as a template for their predictions. By substituting the climate grids for current conditions with climate grids for the

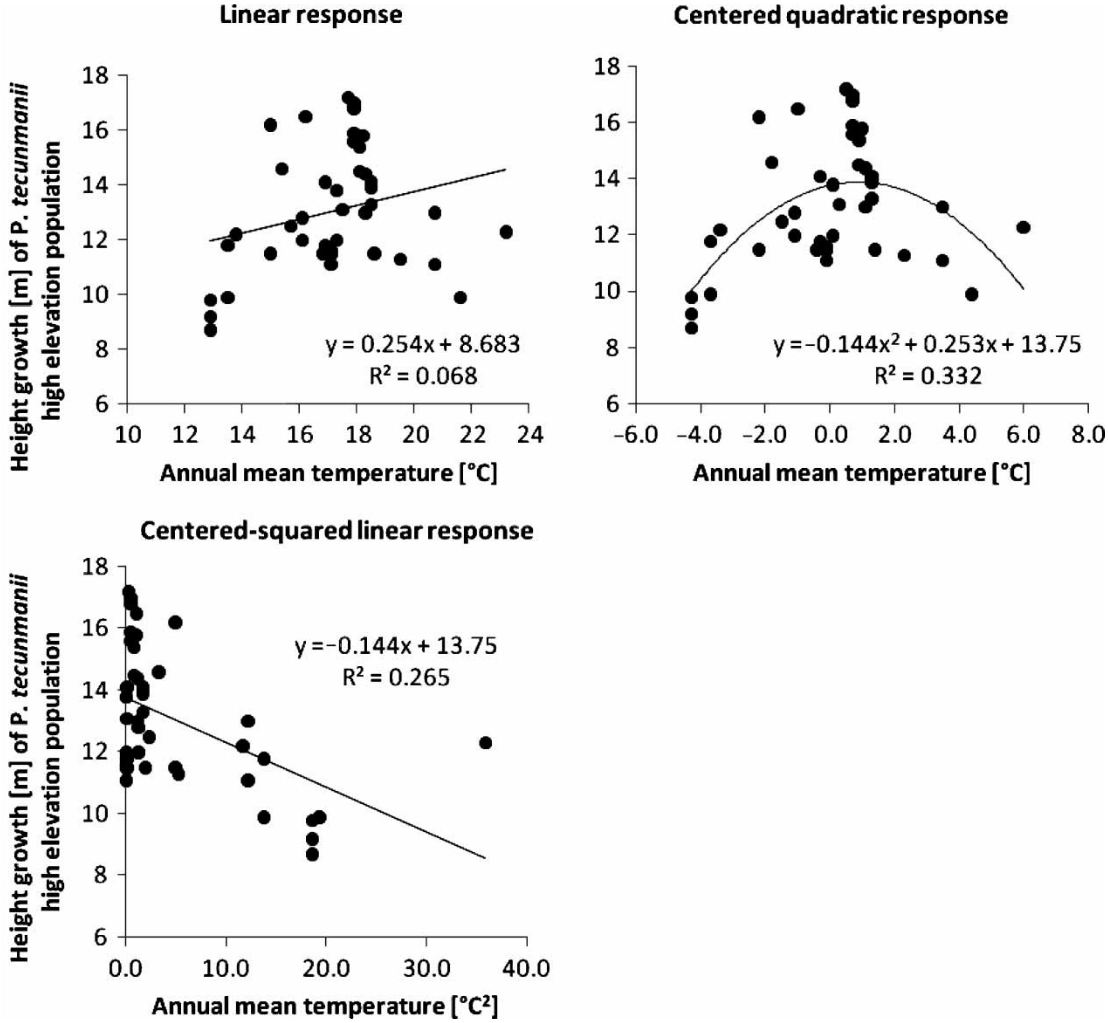

Figure 1. Linear, centred and centred-squared response of *Pinus tecunumanii* high-elevation subpopulation trial's height growth to annual mean temperature. A regression line is drawn through the points. For each plot the coefficient of determination R^2 and according regression equation are given. The sample size n for all three plots is 45.

future, the impact of climate change on the height performance of the plantings by 2020 under the emission scenarios A2a and B2a was inferred. Four 4th assessment GCM runs from the Canadian Centre for Climate Modeling and Analysis (CCCMA), Commonwealth Scientific & Industrial Research Organization (CSIRO), Hadley Centre Coupled Climate Model (HADCM) and National Institute for Environmental Studies (NIES) models were used for the future climate.

To compare height growth of the three taxa under current climate and future climate by 2020, independent t tests were carried with the predicted values at the field trials.

To address variation in projected climate brought about by GCM model uncertainty, the standard deviation of height growth for each variety and ecotype under the four GCM model projections was calculated.

To see whether an adapted planting decision results in a significant improvement in height growth, an independent t test was carried out. The height growth of the three taxa under current and future climate by 2020 was calculated and changes in performance for the best seed choice under current and future climate conditions were tested for their significance.

Results

Model selection and performance

Based on the results of the cross-validation, the most robust model types to predict height growth were selected (Table II). The Linear model type is the most confident model type to predict height growth of *P. patula* var. *patula* and the *P. tecunumanii* lowland ecotype. The Mixed model type proved to be the

Table II. Summary table of cross-validation R^2 scores for the relation between observed and predicted height of test set trials.

	Linear R^2	Squared R^2	Mixed R^2
High	0.096	0.201	0.337
Low	0.512	0.001	0.073
Varpat	0.832	0.812	0.38

Note: The cross-validation results are given for the three modelled genotypes High (*Pinus tecunumanii* high-elevation population), Low (*Pinus tecunumanii* low-elevation population) and Varpat (*Pinus patula* var. patula).

most successful in predicting height growth of the *P. tecunumanii* highland ecotype.

In none of the three model types could a regression equation be developed that significantly predicted 8-year-old height growth of *P. patula* var. *longipedunculata*; coefficient of determination scores (R^2) were 0.22 or lower. Therefore, no site growth predictions were made for this variety. The multiple regression equations for *P. patula* var. *patula*, the *P. tecunumanii* highland and lowland ecotypes yielded R^2 scores of 0.61, 0.62 and 0.56, respectively (and p values of < 0.001, < 0.001 and 0.008, respectively). Variance inflation scores for the three developed models ranged from 5 to 26. The equations are as follows:

Predicted height of the *P. tecunumanii* highland ecotype at age $8 = (-9.3600) + 0.0617^\star$ Cation-exchange capacity of topsoil $+0.1399^\star$ Mean diurnal temperature range $+0.0502^\star$ Annual mean temperature $-0.0545^\star$ Precipitation seasonality.

and

Predicted height of *P. patula* var. *patula* at age $8 = (-19.0058) + 0.0046^\star$ Annual precipitation $+ 0.2054^\star$ Mean diurnal temperature range.

Expected impact of climate change on wood productivity and seed material choice

Under current climate *P. tecunumanii* low-elevation provenances are predicted to exhibit a superior growth performance in the majority of the study area (Figure 2). In Colombia high-elevation provenances of *P. tecunumanii* outperform the other two seed choices at altitudes above 1800 m. In southern Brazil, in the near-coastal areas of the southern Brazilian states of Santa Catarina, Paraná, Sao Paula and Rio de Janeiro, the high-elevation seed sources of *P. tecunumanii* show best height growth. *Pimus patula* var. *patula* is predicted to reach competitive growth rates in the interior of Brazil and South Africa and is able to surpass the fast growing provenances from the low and high-elevation populations of *P. tecunumanii*.

In the overall study area 8-year-old height growth in all three countries is predicted not to change significantly by 2020 (t test, $n = 94$, $m = 49$, $p = 0.4152$). Still, the models predict that in 7.3% of the study area the choice of seed material today should be changed to adapt plantation forestry adequately by 2020.

In Colombia 9.3% of the study area is subject to change, while in South Africa 8.6% and in Brazil 7.4% of the study area is subject to change. Height growth in year 8 is predicted to decline by 0.39 m if seed material is not changed. In those areas height at 8-year-old plantations is predicted to be diminished by 0.39 m if seed material is not changed. A change to the superior choice between the three species/subspecies under future climate will significantly improve this situation by minimizing height loss at year 8 to only -0.04 m (t test, $n = 14$, $m = 14$, $p < 0.0004$).

In 95% of cases the new best choice of seed material is from provenances of the *P. tecunumanii* low ecotype. In Colombia, for example, the area where *P. tecunumanii* lowland ecotypes is predicted to perform best by 2020 moves 80 m higher in altitude. The height of the *P. tecunumanii* low ecotype is predicted to increase by 0.28 cm in 8-year-old plantings by 2020. Provenances from high-elevation seed sources are predicted to be most seriously affected by climate, reducing their average height growth by 1.16 m. *Pinus patula* var. *patula* exhibits comparatively stable growth responses to the environmental changes, losing an average of only 0.14 m in the study area (Table III).

Uncertainty in climate change projections

The standard deviation (σ) of the predicted mean mapped values calculated for the four GCMs serves as an additional indicator for the variability between GCM predictions (Table III). σ and therefore uncertainty of the GCM projections is highest for the site quality model of *P. tecunumanii* low-elevation population. σ values for the studied ecotypes and variety range from 0.25 to 0.4. The evaluation of uncertainty in climate change projections should also take into account the spatial variability in uncertainty. σ between GCM projections calculated for Brazil, Colombia and South Africa independently shows a homogeneous σ of 0.32 for each country.

Discussion

Demand for wood from planted forests is expected to increase in the coming decades (Carle & Holmgren,

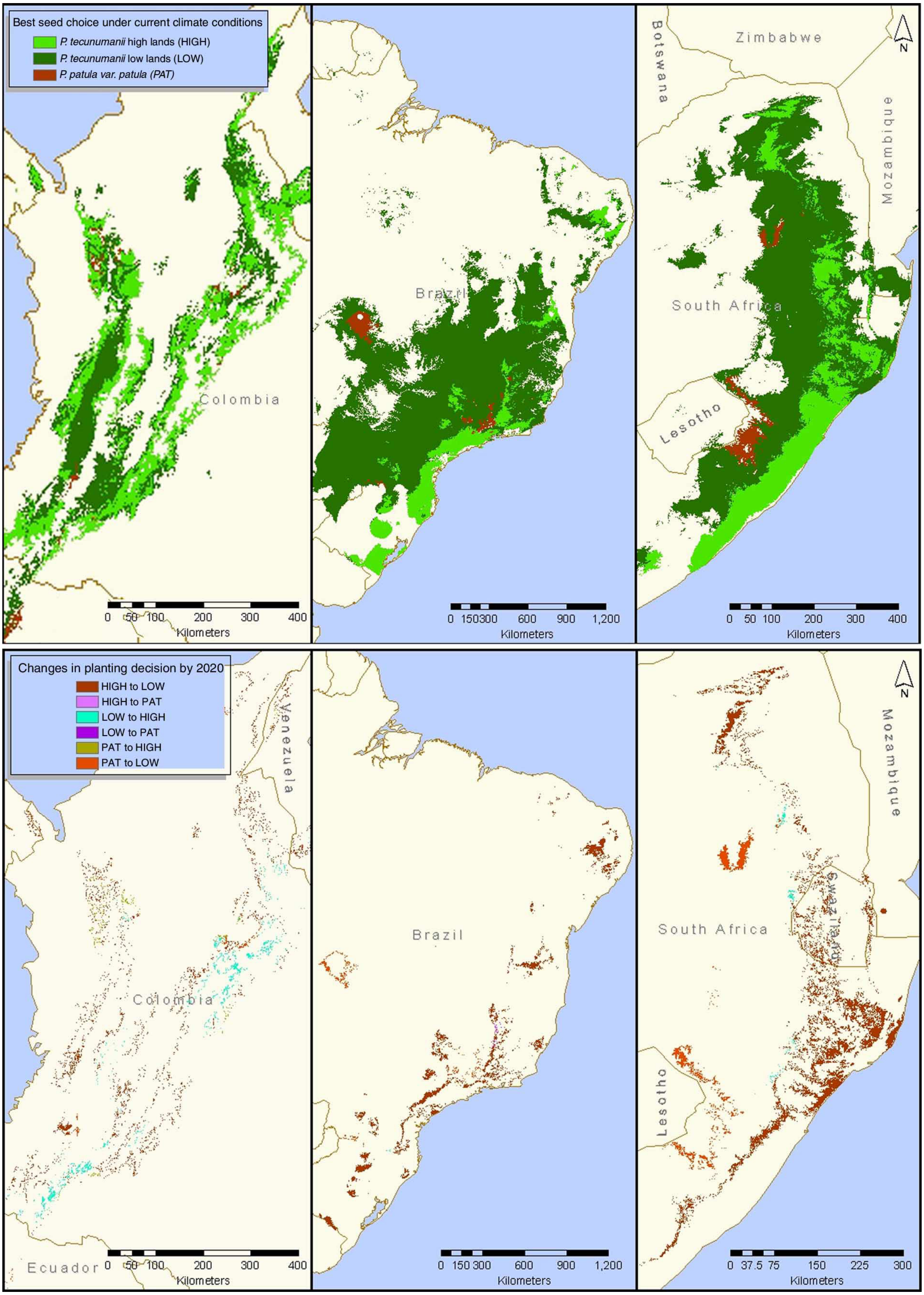

Figure 2. Map of optimal seed choice under current conditions and areas where the optimal planting decision is predicted to change by 2020. The results are based on the average of the results of four general circulation models.

Table III. Map mean values of predicted height growth at the age of 8 years (pht8) for the entire study area.

		CCCMA		CSIRO		HADCM		NIES			
pht8 (m)	Current	△ A2a	△ B2a	△ A2a	△ B2a	△ A2a	△ B2a	△ A2a	△ B2a	Mean △	SD
High	11.7	−0.88	−0.79	−1.04	−1.24	−1.30	−1.17	−1.39	−1.45	−1.16	0.25
Low	14.83	−0.39	−0.24	0.48	0.43	0.50	0.51	0.53	0.43	0.28	0.4
Varpat	11.63	−0.56	−0.51	0.05	0.11	0.08	0.08	−0.17	−0.23	−0.14	0.29

Note: The table shows map mean values for growth prediction models dependent on underlying general circulation model (GCM) and emission scenario—different outcomes of the regression models based on the results of four GCMs: Canadian Centre for Climate Modeling and Analysis (CCCMA), Commonwealth Scientific & Industrial Research Organization (CSIRO), Hadley Centre Coupled Climate Model (HADCM) and National Institute for Environmental Studies (NIES), for two emission scenarios each. The predicted height growth performance under current climate conditions is compared with the anticipated future height growth performance in 2020. Predictions are given for the three modelled genotypes High (*Pinus tecunumanii* high-elevation population), Low (*Pinus tecunumanii* low-elevation population) and Varpat (*Pinus patula* var. *patula*).

2008), while significant wood losses are expected if no appropriate action is undertaken to adapt plantation forestry to climate change (Fairbanks, 1999; Spittlehouse & Stewart, 2003; Kremer, 2007). The importance of selecting appropriate plantation seed material in the face of climate change has been pointed out by Persson (1998) for *Pinus sylvestris* in temperate and boreal plantation forestry. Optimal niches of *P. sylvestris* provenances' height growth are predicted to shift considerably during the next 90 years (Rehfeldt et al., 2002). Fairbanks (1999) points out that especially in *P. patula* and *Pinus radiata* plantations in South Africa a great loss of productivity will occur unless different seed sources are selected that are appropriate for future climate conditions. Through height growth models coupled with future climate scenarios the present report has shown that for 7–10% of areas in the study a change in the most suitable variety or subspecies will occur by 2020 (less than one production cycle away from the present).

Model performance

The developed site quality models for the two *P. tecunumanii* ecotypes and *P. patula* var. *patula* were significant; in particular, the goodness to fit ($R^2_{\text{adj.}}$) of the model for the *P. tecunumanii* lowland ecotype was excellent. No problems are expected in the extrapolation of the model predictions to the whole of study area because this area is within the climate ranges where the field trials are established and cross-validation for all three selected models was significant. The selected model for *P. patula* var. *patula* can be considered very robust since the cross-validation resulted in a high coefficient of determination. The model for the *P. tecunumanii* lowland ecotype was still fairly robust according to the cross-validation and the height growth model predictions also coincided with indicated elevations for optimal growth of this ecotype. Cross-validation of the model for the *P. tecunumanii* highland ecotype resulted in a moderate but still significant coefficient of determination.

In Colombia under current climate conditions a distinct altitude range can be identified at which the height growth of *P. tecunumanii* highland ecotype surpasses the *P. tecunumanii* lowland ecotype growth performance. This threshold ranges from 1300 to 1700 m, coinciding with the altitude that separates the two subpopulations inside their natural distribution range in Honduras (Dvorak et al., 2000). This demonstrates that both ecotypes are best adapted to divergent environments that in each case resemble their respective native niche. This underlines two facts: first, provenances are indeed adapted to their specific environmental conditions; and secondly, it is important to conserve a wide range of seed sources to sustain the value of diversity for plantation forestry in heterogeneous environments and in the face of a changing climate.

For *P. patula* var. *longipedunculata* no significant site quality model could be developed. From the four different taxa studied, the least amount of data was available for *P. patula* var. *longipedunculata*. To improve the prediction of the impact of climate change on height growth for this variety it is recommended to include height data from more field trials established over a wider climate range than could be accessed here.

Impact of climate change on wood productivity and choice of seed material

In general terms no significant changes are predicted by 2020 across the whole study area, but some specific areas important for wood productivity do show significant changes. At these sites a change in seed choice has been shown to adapt the existing planted forests with great effectiveness. Two trials in Santa Tereza, Brazil, for instance were established using seeds from high-elevation populations of *P. tecunumanii.* Observed and predicted heights on this site differ by just 0.05 m. The regression model predicts that on this site low-elevation seed sources would yield the same height growth under current climate conditions. Height growth predictions for the 2020 projections suggest that provenances from the low-elevation population of *P. tecunumanii* will reach 13.7 m in height at 8 years, while the high-elevation population will reach only 12.09 m. This is a significant difference and should be an important criterion used today in selecting seed material for this site.

Pinus tecunumanii lowland ecotype is expected to be the most suitable seed material to plant for the next rotation because of its promising performance under rather hot and wet climates. On sites in South Africa where *P. patula* var. *patula* is planted, seed material from *P. tecunumanii* lowland provenances is either already more suitable or will become more suitable by 2020 (Figure 2).

This analysis concentrated on 2020 climates in order to capture the climate during rotations being planted today. However, the impacts of climate change are expected to become more drastic in the second half of the twenty-first century. The results of this analysis could form the basis for exploring the longer term future of plantation forestry in tropical sites, and evaluate what seed materials are necessary to sustain plantation forestry in Colombia, Brazil and South Africa.

Implications for the conservation of genetic resources

In most plantation areas of Colombia, Brazil and South Africa, seed material of *P. tecunumanii* lowland ecotypes appears to be the best seed choice for wood productivity under the current climate and becomes even more important in the next two decades. However, the analysis also shows the value of diversity, at both the genetic and the species level. Unfortunately, the lowland ecotypes of *P. tecunumanii* in the wild are most threatened by predicted climate change (van Zonneveld et al., 2009*a*). This coincides with studies about the impact of climate change on the natural distribution of other tropical pines that demonstrate that lowland provenances will be most negatively affected by climate change (Sáenz-Romero et al., 2006; van Zonneveld et al., 2009*b*). Appropriate action needs to be taken to conserve these valuable genetic resources. Sáenz-Romero et al. (2006) propose seed transfer of lowland *P. oocarpa* provenances in the wild to higher altitudes in the natural distribution of this species. Another possibility is conservation outside its natural distribution ranges in climate-proofed conservation parks (van Zonneveld et al., 2009*a*). CAMCORE members are currently establishing conservation parks to protect provenances of economically important tree species (CAMCORE, 2009). Further studies could broaden the analysis to look at other factors, and link with economic models to evaluate the true cost of adaptation of plantation forestry and support management plans.

Evaluation criteria for tree performance

The site quality models in this study only incorporate height growth to assess the quality of the sites. This is one of the most important commercial characteristics, but other criteria are also important when evaluating the potential of different provenances. These include stem form, aberrant growth appearances, disease tolerance, resin content and branching or rooting characteristics. Of particular importance is the issue of frequent stem breakage, which is frequently observed in *P. tecunumanii* plantations, where on the worst sites 30–40% of the trees are affected. The propensity for the main stem to break in its upper crown is thought to be the greatest limitation to using *P. tecunumanii* in the tropics and subtropics (Dvorak et al., 2001*a*).

Disease tolerance is another critical characteristic that eventually determines the value of the seed material for future plantation projects. The success of exotic tree species has generally been attributed to effective species–site matching and their freedom from insect pests and diseases in tropical plantations. There is now the fear that climate change will induce catastrophic outbreaks of pests and diseases in native and exotic forest plantations. The consideration of biotic risk factors could greatly improve the applicability of future site quality models.

Conclusions

In this study the need to change the currently used seed material of *P. patula* and *P. tecunumanii* in the existing plantation areas was evaluated to optimize wood productivity in the face of climate change in the next rotations. Overall, no significant changes in wood productivity are predicted. Still, several forestry areas are substantially impacted. In those areas a change to a better adapted seed material is expected to sustain wood products under a changing climate. Provenances of *P. tecunumanii* low-elevation ecotypes are already important sources of seed material and are predicted to be become an even more important seed material by 2020 because of their good performance under the warmer and wetter climate conditions predicted for the future.

The models presented here form the basis for developing site-specific decision support models for selecting planting material under a dynamic climate.

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Article

Selection of Provenances to Adapt Tropical Pine Forestry to Climate Change on the Basis of Climate Analogs

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Abstract: *Pinus patula* and *Pinus tecunumanii* play an important role in the forestry sector in the tropics and subtropics and, in recent decades, members of the International Tree Breeding and Conservation Program (Camcore) at North Carolina State University have established large, multi-site provenance trials for these pine species. The data collected in these trials provide valuable information about species and provenance choice for plantation establishment in many regions with different climates. Since climate is changing rapidly, it may become increasingly difficult to choose the right species and provenance to plant. In this study, growth performance of plantings in Colombia, Brazil and South Africa was correlated to the degree of climatic dissimilarity between planting sites. Results are used to assess the suitability of seed material under a changing climate for four *P. patula* provenances and six *P. tecunumanii* provenances. For each provenance, climate dissimilarities based on standardized Euclidean distances were calculated and statistically related to growth performances. We evaluated the two methods of quantifying climate dissimilarity with extensive field data based on the goodness of fit and statistical significance of the climate distance relation to differences in height growth. The best method was then used as a predictor of a provenance change in height growth. The provenance-specific models were used to predict provenance performance under different climate change scenarios. The developed provenance-specific models were able to significantly relate climate similarity to different growth performances for five out of six *P. tecunumanii* provenances. For *P. patula* provenances, we did not find any correlation. Results point towards the importance of the identification of sites with stable climates where high yields are achievable. In such sites, fast-growing *P. tecunumanii* provenances with a high but narrow growth optimum can be planted. At sites with climate change of uncertain direction and magnitude, the choice of *P. patula* provenances, with greater tolerance towards different temperature and precipitation regimes, is recommended. Our results indicate that the analysis of provenance trial data with climate similarity models helps us to (1) maintain plantation productivity in a rapidly changing environment; and (2) improve our understanding of tree species' adaptation to a changing climate.

Keywords: provenance trials; site quality modelling; management decision support tools; climate similarity; growth prediction

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1. Introduction

1.1. Background

Climate change, and the associated shifts and changes in temperature and precipitation patterns, are likely to affect substantial areas of forest plantation production in the tropics and subtropics. Progressive climate change may make the choice of which species and provenance to plant increasingly difficult. Statistical models, as well as process- and ecophysiologically-based models, suggest a substantial loss of production in plantation forestry, unless appropriate action is taken. It is common practice to choose seed material which is climatically suited to the planting site. However, if climate change proceeds as predicted [1], seed material that is well matched under the current climate will grow in sub-optimal conditions within the production cycles of the upcoming decades [2]. Forest plantations will need to take anticipated climate conditions into account in order to maintain productivity in future harvest cycles. Therefore, seed material, adapted to the novel climate conditions, needs to be immediately identified and selected [3,4]. Sustaining production by identifying the right seed sources for specific sites needs to happen in a time where planted forests become increasingly important to meeting global wood demand and potentially relieving pressure on natural forests in the face of growing demand and dwindling supplies [5–7]. Furthermore, the potential of planted forests to sequester substantial amounts of carbon constitutes an important cornerstone in global climate change mitigation strategies (e.g., [8,9]).

International multi-site provenance trials that measure growth performances of different seed sources in a range of different climates, provide a wealth of information on the adaptive capacity of species provenances that may facilitate selection of seed material for changing climate conditions. Camcore, North Carolina State University (International Tree Breeding and Conservation Program) collected seeds from 40 tropical and subtropical tree species in natural stands. In the last three decades, these seed collections were used to establish more than 1000 ha of field trials [10]. Data from these trials, coupled with high resolution climate data, provides useful information to predict how the growth of economically important plantation tree species is affected by progressive climate change.

1.2. The Analogue Method

Climate analogs are a promising approach to assess differences in provenance performance and their relation to climatic factors. A spatial climate analog in our context, where we want to know which provenance to plant in future climates, draws insights from a location where knowledge on the interaction of climate and tree growth exists and relates these insights to locations in other areas with a similar climate. A temporal climate analog analyses knowledge on past interactions between climate and growth performance to develop an understanding of the present day and make inferences about the future [11,12]. The analog method can help to identify spatial and temporal analog sites to provide insights into the vulnerability of crops or species to climate change, support field evaluation, and create a network through which knowledge on well-adapted cultivars can be passed on. The analog method may also prove to be a very useful tool in pointing decision makers in the forestry sector in the right direction—to support a rational planting decision and sustain, or even improve, wood production in a rapidly changing environment.

Calculating climate dissimilarities (identifying locations which resemble current climate conditions that are expected to be encountered at another location in the future) for the purpose of providing decision support in a changing environment has lately received a great deal of attention (e.g., [13–15]). In the forestry sector, the concept of identifying similarities in climate to match forest seed material to certain sites, in order to assist species selection, is a well-established approach (e.g., [16–18]).

1.3. Research Objectives

In this study, we assess the extent to which the climate analog method can provide concrete recommendations to adapt planted forests to climate change through a better use of forest genetic resources. We ascertain this question in a case study in which we test the ability of this approach to relate climate dissimilarity to the trial’s growth performance. This approach lets us identify appropriate seed material of *P. patula* and *P. tecunumanii* for degraded areas and established planted forests in Colombia, Brazil and South Africa.

First, we evaluated with *P. patula* and *P. tecunumanii* provenance trial data, which, with two ways to measure climate dissimilarity, correlates better with provenance height growth. Secondly, we show how the analog method that resulted in dissimilarity measures that correlated better with height can be used to identify well-adapted provenances for specific plantation sites. We use *P. patula* and *P. tecunumanii* as model species to demonstrate the potential and the restrictions in the application of climate analogs to support management plans to adapt existing and planned forest plantations with expected harvest times around 2030 and 2050.

2. Experimental Section

2.1. Camcore's International Provenance Trial Data

The comparison and validation of the two analog methodologies was based on height growth data from ten provenances of *P. patula* and P. *tecunumanii* at age eight, measured at several test sites (ranging from six to 22 sites depending on the provenance). The data were retrieved from a database of 153 geo-referenced provenance trials, established by CAMCORE members in Colombia, Brazil and South Africa during 1981 and 1997 [10,19,20]. Coordinates were carefully checked following Hijmans *et al.* [21] and are considered to be correct. All trials were measured for height [m], diameter at breast height (dbh) [cm] and survival. Trial management, such as site preparation, spacing of trees, weed control, thinning, and pruning was as similar as practical in the field.

2.2. Study Species' Description

The two closed-cone pine species *P. patula* and *P. tecunumanii* are native to Mesoamerica. Both play an important role as plantation species for the forestry sector in the tropics and subtropics, which is typically lacking adequate resources of coniferous wood. *Pinus patula* is one of the most planted pine species, with close to one million ha established in productive forest plantations [22]. Lesser amounts of *P. tecunumanii* are used in plantations, but it is an important plantation species in Colombia and due to its favorable growth characteristics and comparatively high resistance against pitch canker [23], the species is gaining importance in Brazil and Southern Africa [24]. The natural distribution range of *Pinus patula* extends from the mountainous regions of the state of Tamaulipas in Mexico's East to Veracruz in the country's south. The species can be divided into the two varieties *P. patula* var. *patula* and *P. patula* var. *longipedunculata* [24]. Individual provenances of *P. patula* contain seeds from both varieties. *P. tecunumanii* natural distribution range extends from Chiapas, Mexico to Nicaragua. The species can be divided into two ecotypes based on the altitude where they occur. A highland ecotype (HE) is found in cloud forests at altitudes between 1500 and 2900 m.a.s.l., and a lowland ecotype (LE) of *P. tecunumanii* occurs at altitudes between 450 and 1500 m.a.s.l. [25]. These ecotypes have also shown to be genetically different in molecular marker analysis [26].

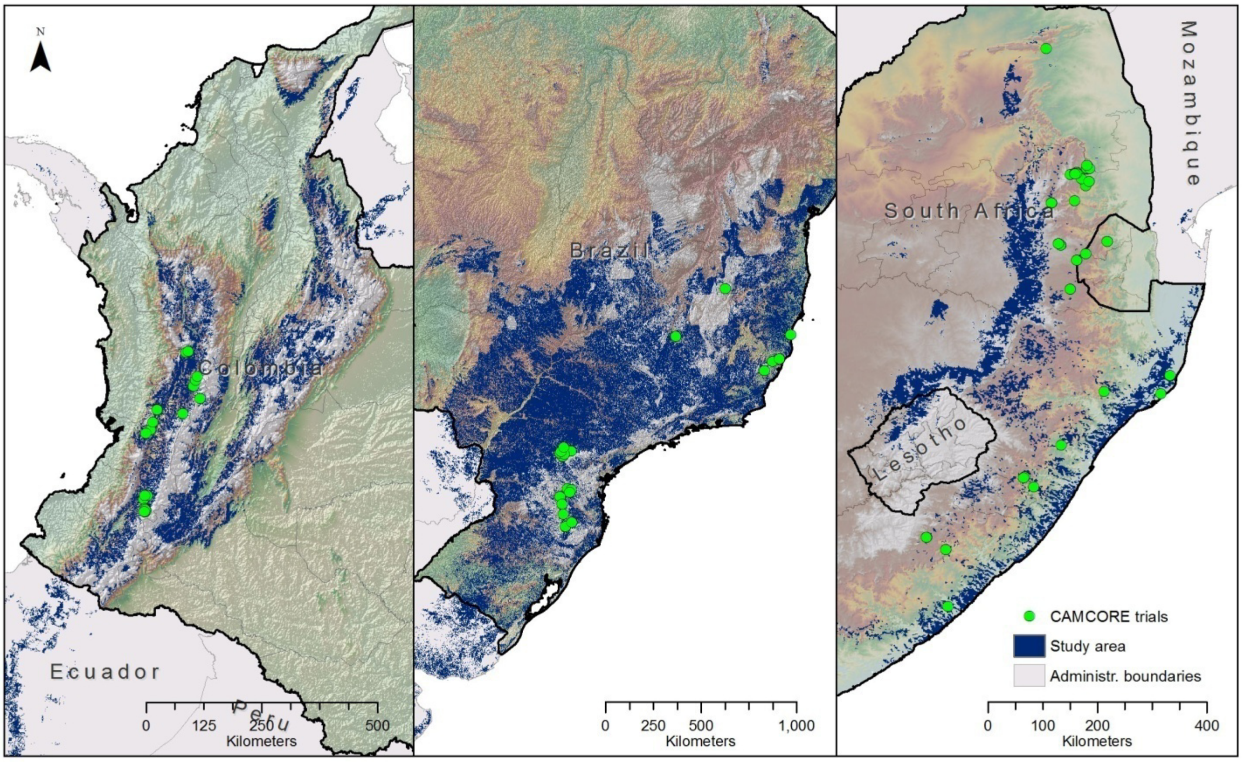
2.3. The Study Area

The study area is restricted to cultivated and degraded areas that are suitable for *P. patula* and *P. tecunumanii* plantations. The area selected for this study comprises a topographic range from 51 m below sea level to 3371 m of altitude and diverse climates that range from tropical conditions in the Colombian highlands, where annual rainfall frequently exceeds 3000 mm, to the dry, subtropical conditions characterized by cold and dry winters in subtemperate South Africa. The maximum annual mean temperature there exceeds 20 °C, but temperature seasonality is more than 10 times as high as in Colombia. In South Africa, in the coldest quarter of the year, the temperature drops below 0 °C. The trials were planted by Camcore partners in parts of the northern tropical Andes in Colombia, and in southern Brazil, where trials are established in the states of Minas Gerais, Epirito Santo, Parana and

Santa Catarina. Trial sites in South Africa are located in the country's eastern escarpment from the Eastern Cape Province to Mpumalanga Province.

A so-called *mask* was developed that only comprises areas which have a similar bioclimatic setup to the climate in which trials, with high survival rates, were established. The study area is restricted to a bioclimatic niche where the species exhibited a survival rate of at least 70% (Figure 1). This bioclimatic niche was confined by maximum and minimum values of five variables derived from trial sites where species exhibited high survival rates. The five variables used to confine the study area (annual mean temperature, maximum mean temperature of the warmest and coldest month, annual precipitation, and precipitation seasonality) are all known to be of physiological importance to the species [27,28]. The masked area was further reduced by excluding all protected areas based on the World Database of Protected Areas [29]. We used global land cover data to restrict the study area to agricultural crop, or managed land [30–32]. In this way we avoid planting suggestions that would promote undesired land-use changes such as of biodiversity-rich Colombian Andean, Brazilian Atlantic and South African landscapes into planted forests.

Figure 1. Map of study area and location of Camcore's provenance trials.



2.4. Climate Data

Current climate data, used to define sites with conditions with similar climatic conditions were derived from the WorldClim database with interpolated climate data from 1960–1990 [33]. The interpolated climate surfaces have a resolution of five arc-minutes which, at the equator, equals approximately 85 km^2. Variables from the database included in this study are monthly total precipitation, monthly mean temperature, diurnal temperature range and 19 derived bioclimatic variables [34].

We use an ensemble of General Circulation Models (GCMs) to develop climate layers for 2030's and 2050's future climate (Table 1). We use three emission scenarios to account for uncertainties in global socioeconomic developments (15 GCM for scenario A1b, 12 for A2 and 14 for B1). These scenarios allow for variations in variables that are related to human population and economic growth and the degree at which technological advances are developed, implemented and exchanged. The three scenarios used in this study are taken from IPCCs 4th special report on Emission Scenarios [3] and reflect the following:

1. a homogeneous world with rapid economic growth that relies on a balance of all energy sources (emission scenario A1b);
2. a more divided world with focus on regionally oriented economic development and slower and more fragmented technological changes (emission scenario A2);
3. an integrated world that is more ecologically friendly and emphasizes global solutions to achieve economic, social and environmental stability (emission scenario B1) [3].

Table 1. List of 20 GCMs used to calculate of climatic dissimilarities for the year 2030 and 2050.

GCM	Developed by	Institute-/Model Name
BCCR-BCM 2.0	Bjerknes Centre for Climate Research	University of Bergen, Norway
CNRM-CM 3	Centre Européen de Recherche et de Formation Avancée en Calcul Scientifique	Centre National de la Recherche Scientifique
GFDL CM 2.0 and 2.1	Geophysical Fluid Dynamics Laboratory	National Oceanic and Atmospheric Administration
GISS Model ER and AOM	Goddard Institute for Space Studies	National Aeronautics and Space Administration
IPSL CM 4	Institute Pierre Simon Laplace	Centre National de la Recherche Scientifique
MIUB ECHO-G	Meteorologisches Institut der Universität Bonn	Friedrich-Wilhelms Universität Bonn
NCAR CCM 3.0	National Center for Atmospheric Research	Community Climate System Model
CCCMA CGCM 3.1 t46 and t63	Canadian Centre for Climate Modelling and Analysis	Meteorological Service of Canada
CSIRO Mk 3.0 and 3.5	Commonwealth Scientific and Industrial Research Organisation	Marine and Atmospheric Research Laboratories
IAP FGOALS g1.0	Institute of Atmospheric Physics	Chinese Academy of Sciences
MIROC 3.2 Hires and Medres	Centre for Climate System Research, Tokyo	Model for Interdisciplinary Research On Climate
MPI ECHAM 5	Max Planck Institute for Meteorology	European Centre Hamburg Model
UKMO HADCM 3	United Kingdom Meteorological Office	Hadley Centre Climate Model
INM CM 3.0	Institute of Numerical Mathematics	Russian Academy of Science
MRI CGCM 2.3 2a	Meteorological Research Institute, Japan	Coupled General Circulation Model

2.5. Data Preparation

For each pair of trials of the same provenance, climate distances were calculated for the current climate and the expected climate in 2030 and 2050. We compared two methodologies using current climate data to calculate dissimilarities. The method that provides the strongest relationship between performance and climate distance was selected to project results into the future. Geographical Information Systems (GIS) were used to import the gridded dataset from R to map model predictions for forestry productions areas [35,36].

For six *P. tecunumanii* and four *P. patula* provenances, there was sufficient information available to develop a model (Table 2).

Table 2. Provenances' identification number, name, species, subpopulation, country of origin and number of trials where it was evaluated.

Id Number	Provenance Name	Species	Subpopulation/ Variety	Country, State of Origin	No of Trials
1	Jocón	*P. tecunumanii*	low elevation	Honduras, Yoro	9
2	Campamento	*P. tecunumanii*	low elevation	Honduras, Olancho	7
3	Chempil	*P. tecunumanii*	high elevation	Mexico, Chiapas	6
4	San Jerónimo	*P. tecunumanii*	high elevation	Guatemala, Baja Verapaz	9
5	Mountain Pine Ridge	*P. tecunumanii*	low elevation	Belize, Cayo	6
6	Sierra Huayacocotla	*P. patula*	*Patula*	Mexico, Veracruz	9
7	Potrero de Monroy	*P. patula*	*Patula*	Mexico, Veracruz	22
8	Chanal	*P. tecunumanii*	high elevation	Mexico, Chiapas	11
9	El Cielo	*P. patula*	*Patula*	Mexico, Tamaulipas	7
10	Conrado Castillo	*P. patula*	*Patula*	Mexico, Tamaulipas	14

2.6. The Analog Methods

The methods we use in this study were developed as part of a joint collaboration between the Walker Institute at the University of Reading, the International Center for Tropical Agriculture (CIAT), and the Climate Impacts Group at the University of Leeds. We compare two implementations that differ in the way environmental parameters are used to compute climate similarities and evaluate which set of climate similarity measures relate better to provenance growth performance. We termed the first method CCAFS dissimilarity. The second method computes dissimilarities with stepwise selected BIOCLIM variables.

2.6.1. CCAFS Dissimilarity, Hereafter Method A

CCAFS dissimilarity's computation closely follows a metric that Williams [13] used to identify climate states with no current analog and disappearance of extant climates. To describe similar climate conditions, Williams [13] referred to four climate variables: mean surface air temperature and precipitation from June to August and from December to February. The equation he uses calculates Standard Euclidean Distances (SEDs) between a pair of sites [1]:

$$SED_{ij} = \left(\sum_{k=1}^{n} \frac{\left(b_{kj} - a_{kj}\right)^2}{s_{kj}^2} \right) \qquad (1)$$

where a_{kj} is the value for climate variable k under current climate and b_{kj} for future projected climate at gridpoints i and j. s_{kj} is the standard deviation of the interannual variability under the current climate [13].

The CCAFS dissimilarity method that was used in this study also computes Euclidean distances, but uses monthly mean values of temperature, precipitation and diurnal temperature range to express climate dissimilarities. Future and present climates are described as m sequential temperature and precipitation vectors [2]. Dissimilarity is then calculated as Euclidean distance between the variables' vectors for reference (f) and target (p) scenario:

$$CCAFS\ dissimilarity = \min_{0 \le lag \le 11} \left(\sum_{m=1}^{m=12} \frac{DTR_m^f}{DTR_{(m-lag)}^p} \left(T_m^f - T_{(m-lag)}^p\right)^z + \left(P_m^f - P_{(m-lag)}^p\right)^z \right)^{\frac{1}{z}} \qquad (2)$$

where DTR is diurnal temperature range, T is temperature, P is precipitation, m is month, p is present and f is future. The time lag searches across 12 months for minimum dissimilarities to capture the fact that not all locations experience the same timing in seasonal variation [37]. The z parameter can be varied to perform a sensitivity analysis, but, in this study, the z parameter was kept constant at 2 to calculate standard Euclidean distances. This metric weighs temperature differences by the quotient of the respective diurnal temperature ranges. The calculated value is termed dissimilarity—instead of a similarity value—to conveniently follow the scaling of the CCAFS measure, where higher values indicate a more dissimilar pair of sites.

2.6.2. CCAFS with Stepwise Selected BIOCLIM Variables, Hereafter Method B

For the second method, only climate variables are used for the computation of dissimilarities that are significantly related to height growth. The stepwise regression used to identify these variables is a common method in variable selection for site growth models [38–40]. All calculations were done in R [35]. The retention criterion was set to be Bayesian Information Criterion (BIC).

Some environmental variables predicted height growth best through a quadratic regression. To enable the multiple linear regression model to account for these quadratic effects, the stepwise regression picked from a pool of variables that contained the linear as well as the centered squared version of the 19 bioclimatic variables. The development of squared centered variables is a recommended method to improve linear regression models in the presence of quadratic effects [41]. To guard against the negative effects of multicollinearity on the stability of regression coefficients and significance levels [42], variance inflation factors (Vif) were calculated. Variables were taken out of the modeling process if their Vif-score exceeded 10, which is a common threshold to test for multicollinearity [43]. Regression equations were tested using a five-fold cross-validation, and the mean square error for each multiple linear regression function was denoted.

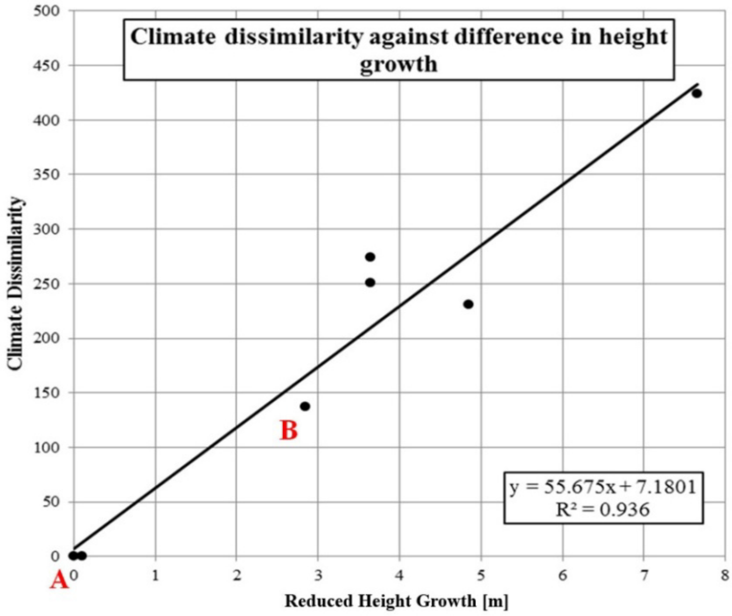
The climate variables found by the stepwise regression for each provenance were then used as input variables to compute SEDs following the CCAFS method adapted to the variables selected via stepwise regression [2].

2.7. Evaluating Dissimilarities in Climate as a Provenance Performance Indicator

We calculate dissimilarity values for each provenance and method for the gridded study area.

We use for each provenance the best performing site as a reference point for the grid calculation (point A) because of the following reasons. (1) Practically, the forestry sector should be interested in climate analogs in order to optimize performance at each location; and (2) We therefore hypothesize that each provenance has an optimum climate for height growth and that height growth reduces when climate varies drastically from the optimal climate. To test our hypothesis, we calculated 10 dissimilarity grids, one for each provenance, and in each case used the coordinates of the most successful trial as a reference. Climate dissimilarity values calculated for coordinates where remaining trials of the same provenance were planted should be clearly related to differences in height growth. If our hypothesis is true, the differences in height performance relative to the best trial should show a significant correlation with the calculated dissimilarity value for each of the trials where the provenance was planted. The goodness of fit of this correlation expresses how well the calculation of climate dissimilarities relates to provenance performance (Figure 2). The linear regression example accounts for 93.6% of the variability in the variable height growth ($R^2 = 0.936$). The point marked A indicates the reference trial with top height growth for which climate dissimilarities have been calculated. The point marked B indicates a trial planted with seeds from the same provenance, in this case *P. tecunumanii* provenance Campamento, at another location. This trial B exhibited 2.85 m less height growth as compared to the top trial (A) and is found at a location associated with a climate dissimilarity value of 137 as compared to the climate found at the location of the top trial.

Figure 2. Scatter plot exemplifying the linear correlation of climate dissimilarity and height growth for one single provenance.



2.8. Spatialization of Results and Growth Predictions

The analog method that is found to provide climate dissimilarity values that most successfully relate to provenance growth differences is used to predict provenances' height growths under current and future climate conditions. The evaluation was based on goodness of fit (R^2) and statistical significance of the relationship.

To estimate growth performances during the next two rotations, the study considers projected climate conditions for the years 2030 and 2050 [44]. Three global socioeconomic development paths are considered by running the analog tool for three SRES emission scenarios: A1b, A2, and B1 for each GCM [45].

Climate dissimilarity was computed in **two** ASCII grids for every provenance (10 in total), time step (current climate conditions, 2030s, 2050s) and for each GCM model. The **first** grid indicates which trial is climatically most similar to a site of interest. The **second** grid calculates a dissimilarity value for this site of interest and the trial indicated by the first grid. Each GCM yields a slightly different dissimilarity value for a pair of sites. The first grid's value can be directly linked to one certain Camcore trial indicating a climatically most similar provenance and, with this, an expected height growth. The projections of the dissimilarity values are all done with climate grids that have a spatial resolution of five arc minutes.

The dissimilarity value from the second grid is used to further refine the result and to estimate height growth of climatically most similar provenance in that specific grid cell. The provenance-specific response functions developed for the analog methodology indicate how sensible the height growth of specific provenances is to climate dissimilarities from their optimal climate (Figure 2). The slope of the linear regression trend line serves as an estimator of this sensitivity. The steeper this slope the less sensitive height growth of a specific provenance is to climate dissimilarities from their optimal climate. Following the linear regression equation [3]:

$$Y = a + bx \tag{3}$$

where Y, the dependent variable, is the dissimilarity in climate from the reference trial, a the intercept and b the slope.

By dividing the slope (b) of the provenance response function with the dissimilarity value (Y) of a certain site, we compute the deviation from the height estimation brought about by climate dissimilarity (x). This deviation subtracted from the height, measured at the climatically most similar trial, gives us the minimum height a provenance is expected to yield at any site inside the study area.

Uncertainties in the simulations of future climate are addressed by comparing the outcomes of the multiple model runs using the different GCMs (listed under Table 1) We assumed that analog predictions are reliable across the climate models if at least 11 (more than two-thirds) of the individual GCMs calculate the same trial to be the best climate analog for a site. In order to take spatial variability in climate model uncertainty into account [46] uncertainties were individually calculated for Colombia, Brazil and South Africa.

3. Results

3.1. Definition of Study Area

Trials exhibited a survival rate of at least 70% where mean annual temperature was between 12.4 and 24.6 °C, maximum temperature of warmest month does not exceed 33.1 °C and average minimum temperature of the coldest month does not fall below 0 °C. Annual rainfall was in the range of 720 and 2666 mm and precipitation seasonality between 88 and 13. The cultivated and degraded areas comprised in this climatic niche cover an area of 2.37 million km^2. Of this area, 5.75% lies inside the administrative boundaries of Colombia, 84.53% in Brazil, and 9.72% in South Africa, Lesotho, and Swaziland.

3.2. Comparison of Analog Methods in Their Ability to Predict Provenance Performance

The method that provided climate dissimilarity measures that best correlated with growth performance was selected. Selection criteria included the average R^2 of the climate dissimilarity growth performance models by species and whether the provenance-specific relationships between climate dissimilarity and growth performance were statistically significant. Models resulting from using climate dissimilarity measures from method A yielded an average coefficient of determination of 0.68 for *P. tecunumanii* provenances and an average coefficient of determination of 0.12 for *P. patula* provenances. Models resulting from using climate dissimilarity measures from method B had a similar average R^2 value for *P. tecunumanii* provenances of 0.59 and *P. patula* provenances of 0.15 (Table 3). Cross-validation of the method relying on stepwise selected climate variables yielded an average square root residual error of 0.92 m corresponding to an error of 7.5% (mean height of 10 provenances equals 12.28 m) which is considered to fall inside an acceptable error margin. Climate dissimilarity measure from both analog methods can thus be seen to relate equally well to growth differences. It has to be noted that while the stepwise regression algorithm is still commonly used in the field of ecological modeling, its advantages and shortcomings are a topic of recent debate among statisticians [40,47,48]. Since no method is found to be clearly superior in terms of scored R^2 values, method A resulted in a relationship with a larger number of provenances. With respect to *Pinus patula*, only regression functions for the provenance *Sierra Huayacocotla* (6) for standard method A and *Conrado Castillo* (10) for method B were not significant at α 0.1 (Table 3). The values in the table indicate coefficient of determination scores of the 10 regression function developed to validate the two methods. The level of significance is coded according to the regression's *p*-value: 0.001(***), 0.01(**), 0.05(*), 0.1(.), 1( ). All regressions for *P. tecunumanii* developed using the standard CCAFS method, except *Mountain Pine Ridge* (ID 5), are significant at the 0.1 level. Four out of five of these regressions are significant at the 0.01 level.

Table 3. Table summarizing the results of the analog method comparison.

	***Pinus tecunumanii* provenances**							***Pinus patula* provenances**				
	1	2	3	4	5	8	Average$_1$ R^2	6	7	9	10	Average$_2$ R^2
CCAFS	0.79 **	0.94 ***	0.95 ***	0.44 .	0.32	0.66 **	0.68	0.37 .	0.02	0.01	0.10	0.12
BIOCLIM	0.53 *	0.36	0.95 **	0.25	0.77 *	0.70 **	0.59	0.02	0.03	0.19	0.37 *	0.15

Figures 3 and 4 depict the 10 regressions developed for the CCAFS method and the BIOCLIM method, respectively. They depict how well climate dissimilarity expresses differences in tree height growth at age eight for each provenance. The provenance name is indicated above each plot. The dotted line indicates the 5% confidence band for each linear regression. The number in each plot area indicates the regression's coefficient of determination.

Method A was found most useful in relating climate dissimilarities to differences in growth in a selection of pine provenance performances and was chosen to generate spatial climate analogu and project the generated grids of climate dissimilarity into the future.

Figure 3. Results of validation of CCAFS dissimilarity computation.

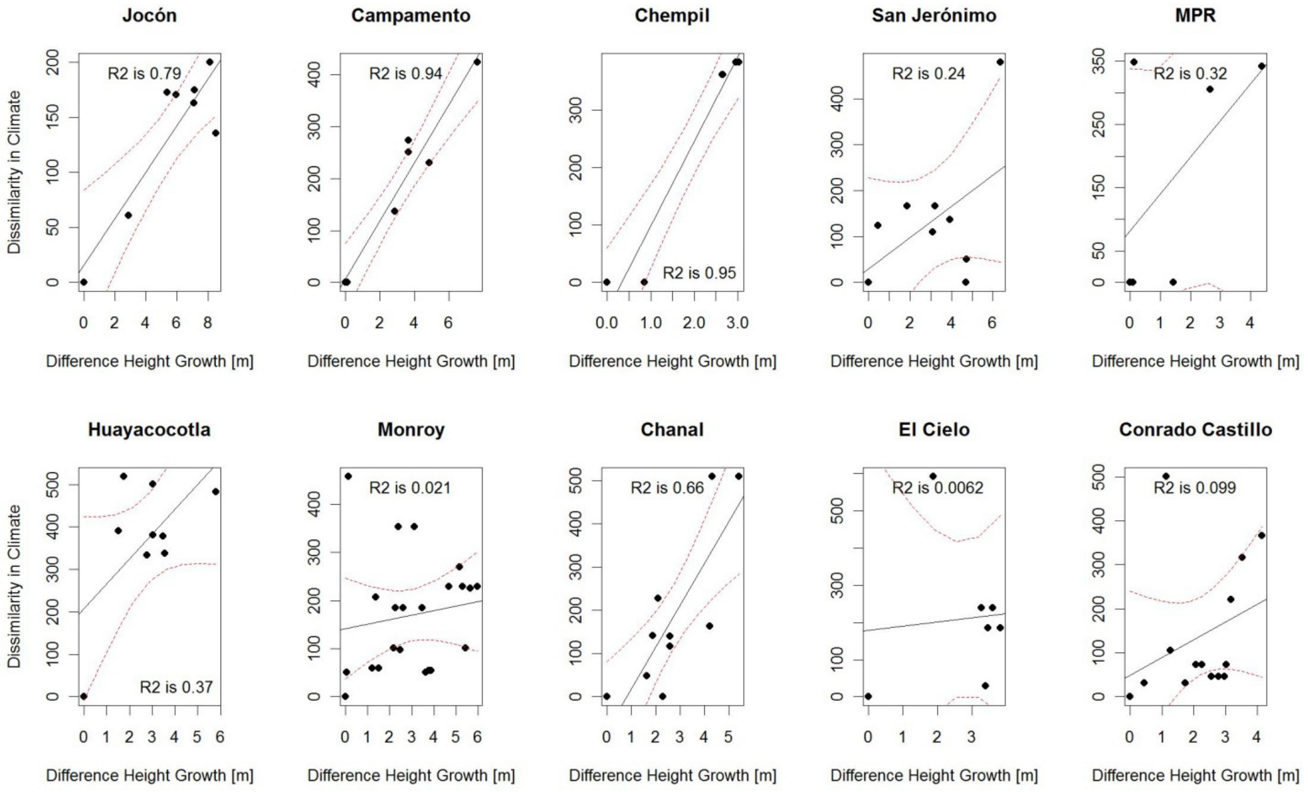
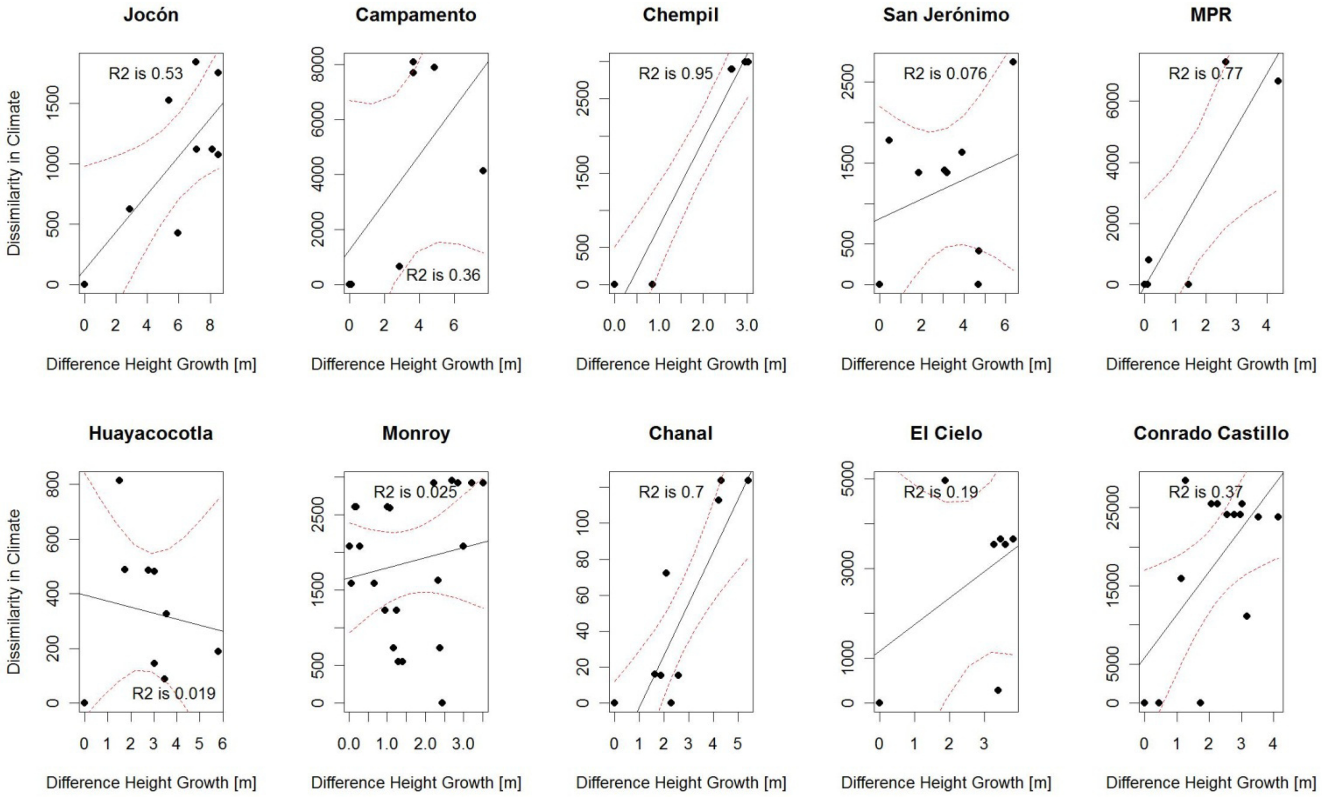


Figure 4. Results of validation of CCAFS dissimilarity with stepwise-selected BIOCLIM variables.



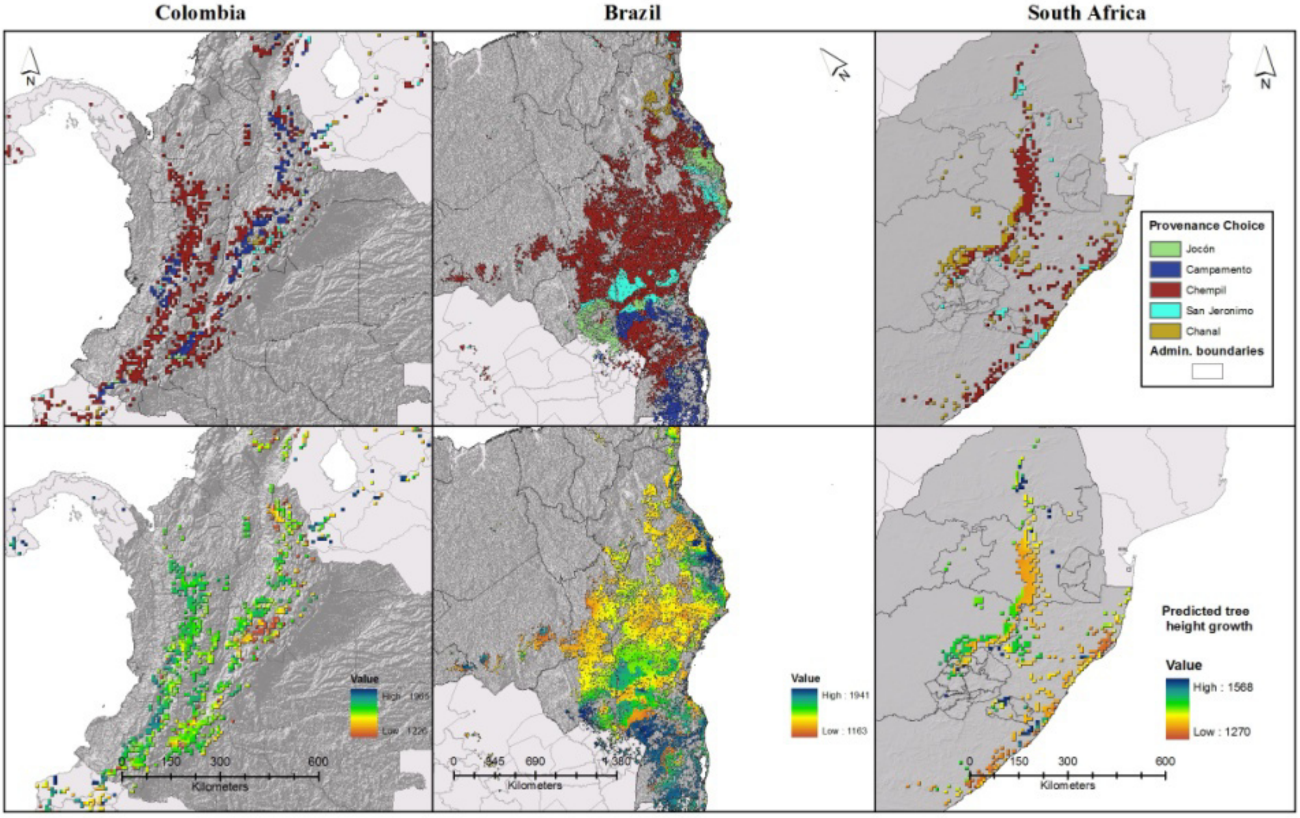
3.3. Expected Impact of Climate Change on Wood Productivity and Choice of Seed Material

Under the current climate, the P. *tecunumanii* HE Chempil is predicted to increase growth performance in 65.9% of the study area (Table 4). In the Colombian states of Valle del Cauca, Santander and Huila, the seeds from the provenance Campamento, originating from Honduras, are predicted to yield the highest growths rates. Campamento is also found to be the fastest-growing provenance when planted in southern Brazil, in the state of Rio Grande do Sul. In the near coastal areas of the central Brazilian states Espirito Santo and Rio de Janeiro, the *P. tecunumanii* LE provenances Jocón and San Jeronimo show the best height growth (Figure 5).

Table 4. Table summarizing model results of best seed choices under current and future climate conditions.

	Current Climate			Change by 2030			Change by 2050		
Provenance	**Colombia**	**Brazil**	**South Africa**	**Colombia**	**Brazil**	**South Africa**	**Colombia**	**Brazil**	**South Africa**
Jocon **	1.94	6.96	0.07	−1.19	−0.89	-	−1.38	−0.67	-
Campamento ***	21.07	14.02	0.04	1.00	2.31	-	2.19	4.02	-
Chempil ***	74.61	69.08	58.23	0.16	−0.74	−2.23	−1.50	−2.16	−9.63
San Jeronimo .	1.57	7.41	10.50	−0.66	−0.01	3.08	−0.60	−0.62	4.45
Huay .	-	-	-	-	-	-	-	-	-
Chanal **	0.82	2.54	31.16	0.69	−0.67	−0.74	1.29	−0.58	5.29

Figure 5. Map of best seed choice and predicted height growth under current climate conditions.



The population Chanal, originating from HE seed sources, are predicted to show favorable growth rates in parts of Eastern Cape provenance and in the northern part of Natal and Zululand. A promising seed source for Swaziland and Mpumalanga province of South Africa is San Jeronimo, from the state of Baja Verapaz in central Guatemala. The best performing *P. patula* provenance according the climate dissimilarity model is Sierra Huayacocotla originating from Veracruz, Mexico. The provenance was not the best seed source for any portion of the geographic area considered. Nevertheless, as the second-best planting alternative, seeds from Sierra Huayacocotla are of importance in 16.2% of the study area.

Climate change is predicted to significantly alter the choice of seed material by 2030 in 14.6% and by 2050 in 18.7% of the study area. In Colombia, the choice of seed material for harvesting between 2020 and 2050 should be changed in 21% of the study area to adapt adequately to these climates. In Brazil, 11.6 and in South Africa 23.3% of the study area is subject to change. By 2050, a change is predicted to be necessary in 23.8% of the study area in Colombia of 17% in Brazil and of 27.8% in South Africa. In Brazil and Colombia, seeds from Jocon slightly lose while seeds, especially from the provenance Campamento, gain importance by 2030. In South Africa, the provenance Chanal is losing while Chempil and San Jeronimo is gaining importance as most suitable seed material (Table 4). The numbers in Table 4 indicate in what percentage of the study area the respective provenance was found to exhibit the highest expected height growth under current climate. The table gives this information for sites in Colombia, Brazil and South Africa separately. The values under column "Change by 2020" and "Change by 2050" show the change brought about by climate change. These values are the average change predicted to occur by the utilized three emission scenarios, a1b, a2, and b1. The symbols next to the provenance names are used to depict the level of significance according to the regression's *p*-value 0.001(***), 0.01(**), 0.05(*), 0.1(.), 1( ).

Selection of material adapted to climate change enables foresters to maintain yield levels. In none of the three studied countries does change in expected height growth exceed 1%. The standard deviation of height predictions, not denoted in Table 5, indicate that while yields are highest in Colombia, so is the study area's heterogeneity in terms of modeled height growth. The numbers in Table 5 indicate expectable height growth (row 1) or change in height growth compared to current climate (row 2 and 3) if seeds from provenances are planted that show best height growth according to the analog model results. The level of significance according to the regression's *p*-value range from 0.05 to 0.001.

Table 5. Estimated average height growth of the most suitable seed sources under current climate and expected change by 2030 and 2050.

	Colombia	**Brazil**	**South Africa**
current climate [m]	15.27	13.62	13.44
change by 2030 [Δm]	−0.19	−0.07	−0.12
change by 2050 [Δm]	−0.35	−0.04	0.02

3.4. Influence of Socioeconomic Scenarios on the Prediction's Outcome

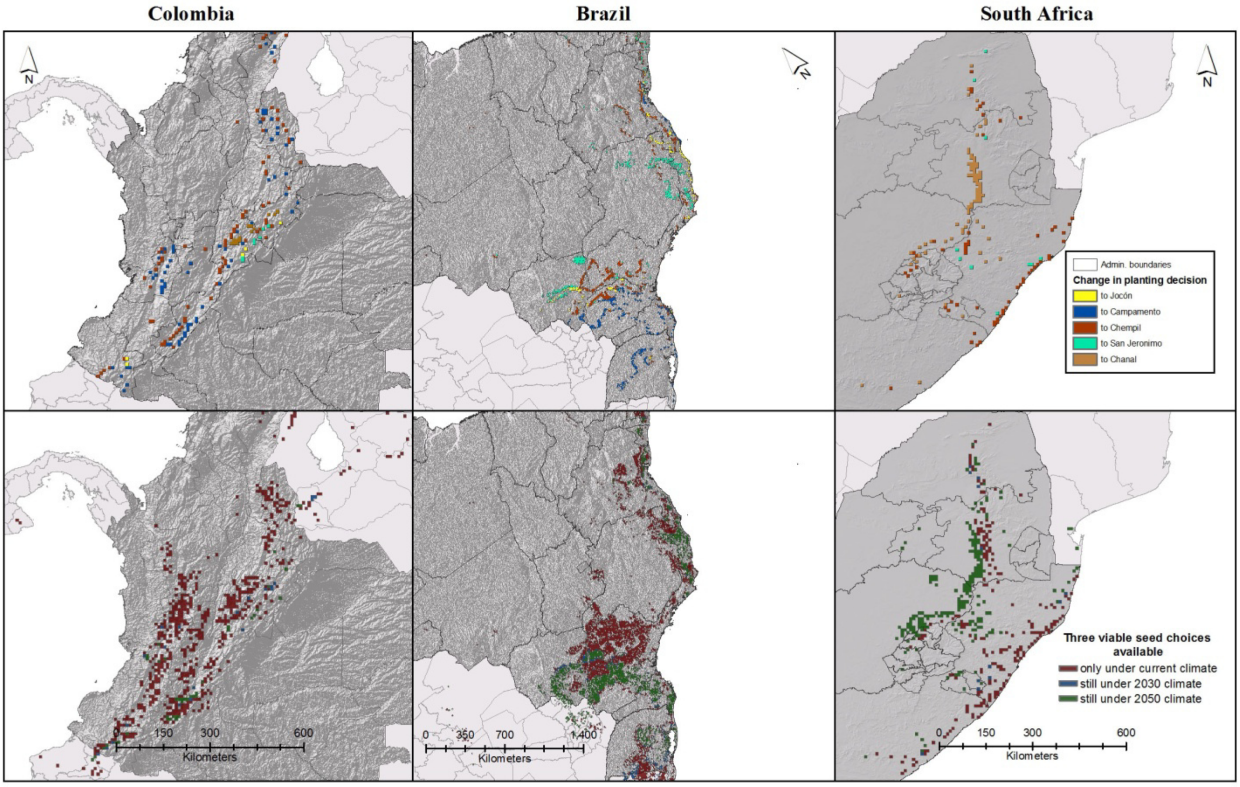
Differences in driving forces and emissions that underlie the projected climates for 2030 and 2050 lead to different predictions in 5.2% of the study areas. The predicted climate in year 2030 for the different emission scenarios influences the planting decision in 5% of study area. Per country, these differences make up 2.1, 5.2 and 12% in Colombia, Brazil and South Africa, respectively. By 2050 the scenario influence on planting decisions more than doubles to 13% of the study area. By 2050, these differences increase to 8.4% globally, or 6.1% in Colombia, 9% in Brazil, and 12.3% in South Africa. Differences in the predictions based on the scenarios A1b and A2 are not significant.

3.5. Available Viable Seed Choices

An important aspect for foresters to select good planting material is not only the height a provenance choice can be expected to grow under certain climates. Many other site factors such as soil characteristics or pressures from biotic threats play an important role, as well. For example, *P. patula* and *P. tecunumanii* do not grow well on poorly drained soils that remain moist. Because our approach does not account for these site factors, we evaluated and here present the best three provenances climatically suitable for a given site. These provenances should be further evaluated for pest resistance or suitability in terms of non-climatic site effects (Figure 6).

The model runs indicate that planting sites in Colombia are most sensitive to the choice of climatically well-matched seed material. Achievable yields are high but seeds should be well adapted to local climate conditions. Expected differences in height growth from the first to second-best seed choice are 4 m and 4.7 m from the 1st to 3rd choice. These differences are predicted to increase slightly until 2030. For sites in South Africa, the model runs predict that difference between the top three seed choices are low with only 1.1 m from best to third choice. Brazil exhibits with 2.1 m an average difference in expected height growth from first to third seed choice.

Figure 6. Spatial results of analog runs for projected climate conditions.



3.6. Uncertainty in Climate Change Projections

As an indicator of variability of the GCM prediction, a level of agreement between the climate models is calculated. We consider a confident level of agreement between GCMs when for all six provenances at least 11 of the 16 models predict the same trial to be climatically most similar to a certain site. A single indicator, as a measure for climate model uncertainty was calculated for each country separately. We summed up the individual level of agreement per provenance and the respective portion of the study area where this level of agreement was found. Climate uncertainties are lowest in Colombia and highest in Brazil. GCM agreement decreases from 2030 to 2050 in Colombia and Brazil by 2.1 and 2.4% respectively while in South Africa agreement increases slightly by 0.3%.

4. Discussion

Wood demand from planted forest increases rapidly [6,49] while at the same time plantations are expected to yield significantly reduced harvestable amount of timber if no appropriate action is undertaken to adapt plantation forestry to climate change [2,50]. The projected climate changes have the potential to alter the distribution of optimal planting areas and seed choices for current cultivars of the major tree crop species. Optimal niches of *P. sylvestris* provenances' height growth in Eurasia and North America are predicted to shift considerably during the next 90 years [51]. Also in *P. patula* and *P. radiata* plantations in South Africa, a great loss of productivity is expected to occur unless different seed sources are selected that are appropriate for future climate conditions [52].

4.1. Climate Dissimilarity as an Estimator for Provenance Performance

Our results show that analog tools that calculate climate dissimilarity measures serve as a useful indicator to determine site–provenance–climate relationships in *P. tecunumanii*. The identification of climatically similar environments, coupled with future climate scenarios, suggests a change in the most suitable provenance for 11 to 23% of the study areas will occur by 2050. The outcomes of the evaluation of climate dissimilarity as provenance performance indicator for *P. patula*, however, suggest that the growth performance of this species is more robust to changes in the considered climate factors. This may indicate, on the one hand, that *P. patula* is less sensitive to changes in climate, but it could also be due to the fact that Camcore's members planted *P. patula* in a climate range that is somewhat more confined than the one occupied by *P. tecunumanii* trials.

The dissimilarity value calculated via the CCAFS method could best be related to height and diameter growth of individual *P. tecunumanii* provenances. The analog methodology based on stepwise found Bioclim variables performed similarly well, but the more robust method is believed to be the CCAFS method (e.g., [47]). It does not only refrain from using the stepwise algorithm, but also accounts for interannual and seasonal variations in climate, which are believed to play an important role in influencing crops and tree growth [53–55].

Individual provenances' growth performance related well to the calculated dissimilarity values (e.g., provenance Jocón, Campamento, Chempil, and Chanal). For *P. tecunumanii*, the study suggests that intra-specific variation and forest plantations' growth rates can be related to the geographic origin of the reproductive material [10,56].

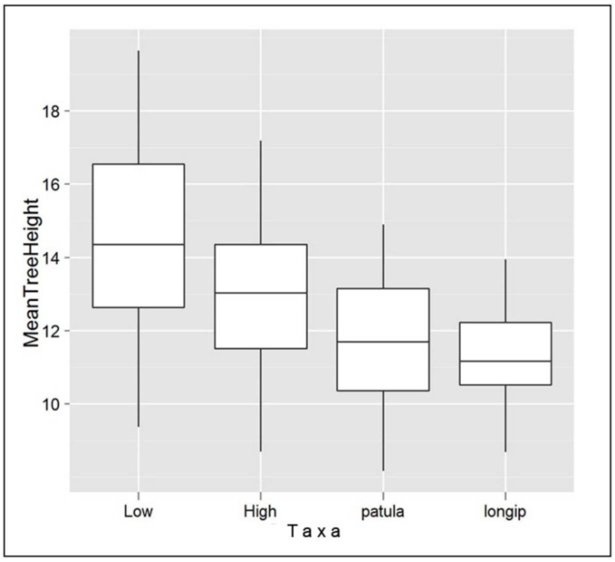
Our analog models calculate statistical, mathematical similarity in climates for sites where successful provenance trials were established and are not bound by the fact that a species in the wild may only realize a fraction of its fundamental niche (e.g., [57]). Developing planting advice from the identification of climate analog to successful trials from multisite provenance tests, avoids a major shortcoming of similarity models that make predictions based on species' natural distribution ranges. These models neglect the incongruity of a species' fundamental and realized niche, whereas the CCAFS analog approach has the possibility to account for the full adaptive capacity of the tested species.

4.2. "Analogues'" Performance in Relation to Species' Stability across Environments

A common approach in tree breeding for assessing a provenance's stability across environments regresses provenance and family means on the mean of the trial site [58]. The underlying thought is that an unstable source would provide higher yields than the "climate safe" stable source. The breeder has to decide if it is better to choose stable or unstable genetic entries for the tree improvement or planting program [59]. A forester faces very much the same situation when selecting a seed source for planting. In the context of climate change, the choice may very well turn in favor of the lower yielding but more reliable source.

The box plot in Figure 7 shows measured height growth for *P. tecunumanii* low elevation subpopulation (Low), *P. tecunumanii* high elevation subpopulation (High) and *P. patula's* two varieties *var. patula* (patula) and *var. longipedunculata* (longip). The upper and lower boundary of the box depict the first and third quartiles, and the line indicates the maximum and minimum measured height. The horizontal line inside the box indicates the height distribution's median. Results from evaluating the relation between climate dissimilarity to growth performance support the specialization hypothesis for phenotypic plasticity (compare [60–62]). This hypothesis postulates that plants that are relatively specialized to a particular environment should exhibit a relatively high magnitude of phenotypic plasticity across a range of alternative environments, particular for characteristics that most closely estimate fitness which, in our study, is height growth.

Figure 7. Box plot of mean height growth at age eight.



The findings (Figure 3 and Figure 4) indicate a relatively large degree of specialization of the *P. tecunumanii* provenances to their natural environment which results in phenotypic instability as they are introduced to new environments. The large standard deviation in *P. tecunumanii* (HE) growth may partly be attributed to stem breakages common for this population [63]. The even larger standard deviation present in the measurements for *P. tecunumanii* (LE), however, cannot be explained by this defect alone (Figure 7). It could partly be the result of the degree of natural introgression with *P. oocarpa* [26], but is more likely than not attributed to LE's large degree of specialization to its environment. Seed material from *P. patula* provenances growing in Mexico at elevations from 1490 to 2920 m, is likely to be adapted to a broader range of climate conditions than the narrowly distributed *P. tecunumanii*, as temperature and precipitation patterns change along the elevation gradient. The "analog" validation results suggest that *P. patula* provenances are rather tolerant to different climate conditions and may be less specialized, or in other terms, less narrowly adapted to a particular climate niche than *P. tecunumanii*'s LE. *P. patula* provenances exhibit a rather low degree of phenotypic plasticity and do not react sensitively to changes in climate in terms of height growth. Different climates evaluated with CCAFS's analog method expressed through temperature, precipitation and diurnal temperature vectors do not seem to trigger *P. patula*'s height or diameter growth (Figure 3).

P. patula's insensitive reaction to a broad range of climates makes it especially valuable in an unstable climate. In the face of great climate uncertainty, and the shortcomings of climate models to reliably predict temperature and precipitation patterns one or two rotations from now, species and provenances should be selected that are not overly sensitive to climate change. The response functions

(Figure 3) developed in this study enabled us to directly ascertain and compare different provenances' climate sensitivity. Coupled with analog or comparable statistical models, provenance tests help to select seed material well adapted to anticipated climate conditions and let us identify genotypes of proven broad adaptability. These are especially valuable in areas where the comparison of GCMs and SRESes indicate that the direction and magnitude of climate change is uncertain. Results such as these indicate once more the enormous value of international trials in obtaining dissemination results of wide application (e.g., [56,57]).

4.3. Implications for Plantation Forestry

A decision model for managing forests under climate uncertainty, and assessing management options for intensively managed forests is necessary to prepare the forestry sector to the challenges of climate change. Our results aim to facilitate part of this decision model for managing forest under rapid environmental change and uncertainties. In view of expected climate instability, adaptability of forest trees causes serious concern due to their long lifespan compared to the rapidity of expected changes in environmental conditions [56,64,65]. Preliminary analysis indicates that concepts and contingency plans for adapting forests are rarely included in national plans for adaptation [66]. The information on climatically well-adapted seed sources and phenotypic plasticity of individual provenances generated in this study may assist rational planting decisions in an uncertain environment (compare [4,9]).

The site quality models include important commercial characteristics like height and diameter growth. Of particular importance when evaluating the potential of different provenances is also the issue of frequent stem breakage. This is repeatedly observed in *P. tecunumanii* HE plantations where on the worst sites 30%–40% of the trees are affected. The propensity for the main stem to break in its upper crown due to a large number of branches produced per whorl and/or wind storms is thought to be the greatest limitation to using *P. tecunumanii* in the tropics and subtropics [10]. Other important traits greatly influencing the planting decision are species and provenance specific susceptibilities to fungi and insects. Including biotic risk factors in the growth and site quality models by identifying environments that favor relevant insects such as *Pineus pini* (woolly aphid), *Cinara cronartii* (black aphid) or fungi such as *Fusarium circinatum* (pitch canker) could greatly improve the applicability of climate-driven decision support models [10]. Results presented in this study provide a good starting point to assist a rational planting decision. Similar climates and sites with well-matched provenances could be identified. In a second step, suggestions can be adjusted to soil types or species-specific preferences in terms of their non-climatic abiotic and biotic environment. Further elaborating the potential of the model to simulate pitch canker-resistant hybrids such as *P. patula* x *P. tecunumanii* could be of great value for the forest industry [67]. One could assume that the hybrid is intermediate between the parents in most traits like frost and drought resistance.

Projection's Uncertainties

There are several considerable uncertainties and a number of possible error sources such as the lack of agreement between climate models [68] or low resolution of climate grids that might be too coarse for case-specific decision support. Nevertheless, the models presented here form the basis for developing site-specific decision support models for selecting planting material under a dynamic climate. In view of the rapid increase of area covered with tree plantations from 264 Mio ha 2010 to more than 300 Mio ha by 2020 [7] the analog tool may provide much-needed decision support for the forest sector in a time where rapid climate change makes the choice of the right seed source increasingly difficult.

The dependence of climate projections on the chosen emission scenario is believed to be low, at least up to the year 2035 [69]. There is no reason to believe that including CO_2 fertilization effects would alter results since there is no scientific evidence that intraspecific variation at the provenance level would exhibit different physiological responses to altered concentrations of CO_2. No problems are expected in the extrapolation of the model predictions to the whole study area because the area is within the climate ranges where the field trials are established.

5. Conclusions

In this study, Analogue, a statistical tool to quantify climate distances, was tested with growth data from international provenance trials. After careful validation, the tool was used to evaluate the need to change the currently used seed material of *P. patula* and *P. tecunumanii* provenances to optimize wood productivity in the face of climate change in the next rotations. Correlation of climate dissimilarity with differences in height growth per provenance allowed us to distinguish between seed sources that have high height growth in a specific climate, like most *P. tecunumanii* provenances, and provenances that have a more moderate height growth but that are adapted to a wide climate range, such as most tested *P. patula* provenances. Although the climate analog may be particularly useful to identify suitable areas for *P. tecunumanii* provenances, *P. patula* provenances may be more convenient to plant in a rapidly changing environment because of their ability to adapt to a wide range of climates.

Competing Interests

The interpretation of data, presentation of results or the conclusions drawn are not influenced by any of the authors' personal or financial relationships.

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