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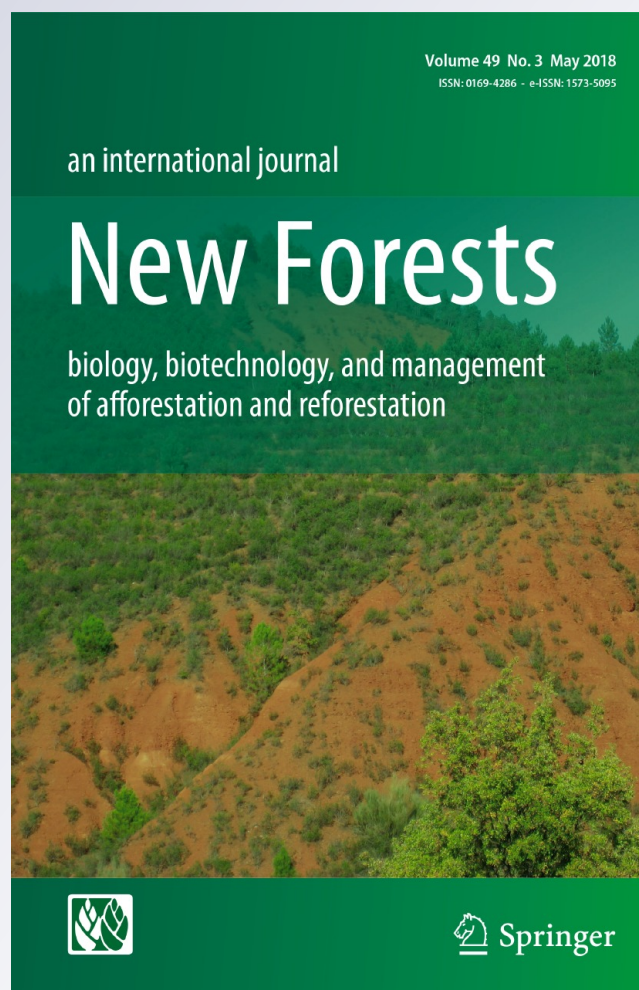
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Climate-based seed zones for Mexico: guiding reforestation under observed and projected climate change

Dante Castellanos-Acuña¹ · Kenneth W. Vance-Borland² ·
 J. Bradley St. Clair³ · Andreas Hamann¹ · Javier López-Upton⁴ ·
 Erika Gómez-Pineda⁵ · Juan Manuel Ortega-Rodríguez⁶ ·
 Cuauhtémoc Sáenz-Romero⁵ 

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Abstract Seed zones for forest tree species are a widely used tool in reforestation programs to ensure that seedlings are well adapted to their planting environments. Here, we propose a climate-based seed zone system for Mexico to address observed and projected climate change. The proposed seed zone classification is based on bands of climate variables often related to genetic adaptation of tree species: mean coldest month temperature (MCMT) and an aridity index (AHM). The overlay of the MCMT and AHM for the 1961–1990 period resulted in 63 climate-based zones. Climate change observed over the

✉ Cuauhtémoc Sáenz-Romero
 csaenzromero@gmail.com

Dante Castellanos-Acuña
 dcastell@ualberta.ca

Kenneth W. Vance-Borland
 kenvb@conspan.net

J. Bradley St. Clair
 bstclair@fs.fed.us

Andreas Hamann
 andreas.hamann@ualberta.ca

Javier López-Upton
 jlopezupton@gmail.com

Erika Gómez-Pineda
 erigomezpin@hotmail.com

Juan Manuel Ortega-Rodríguez
 jmortegarodriguez@icloud.com

¹ Department of Renewable Resources, University of Alberta, Edmonton, AB T6G 2H1, Canada

² The Conservation Planning Institute, 8285 NW Wynoochee Dr, Corvallis, OR 97330-2878, USA

³ USDA Forest Service, Pacific Northwest Research Station, 3200 SW Jefferson Way, Corvallis, OR 97331, USA

⁴ Postgrado en Ciencias Forestales, Colegio de Postgraduados, 56230 Texcoco, México, Mexico

last three decades has resulted in an increase of $+ 0.74\text{ }^{\circ}\text{C}$ for MCMT and a shift toward overall drier conditions across Mexico. By the 2050s, MCMT is expected to increase by $+ 1.7\text{ }^{\circ}\text{C}$ and AHM shifts further towards drier conditions. We recommend moving seed sources from warm, dry locations towards currently wetter and cooler planting sites, to compensate for climate change that has already occurred and is expected to continue for the next decades. We contribute a straight-forward climate-based seed zone system that allows practitioners to match seed procurement regions with planting regions under observed and anticipated climate change. Our transfer recommendations using climate-based zones can be implemented within the existing seed zone system, which often span large climate gradients.

Keywords Climate change adaptation · Reforestation · Seed zones · Seed transfer guidelines

Introduction

Numerous common garden studies indicate that forest tree populations are fundamentally adapted through natural selection to their local climates, primarily cold temperatures and aridity (St Clair et al. 2005; St. Clair 2006; Chmura et al. 2011; Vizcaíno-Palomar et al. 2017). Seed zone delineation for forest tree species is essential to guide where seed may be collected and where corresponding planting stock may be deployed in reforestation programs (either for ecological restoration or commercial plantations), in order to appropriately match locally adapted genotypes to their corresponding environments (Johnson et al. 2004; Dutkowski et al. 2016). Such tasks have become more complicated due to climatic change (Aitken et al. 2008; Castellanos-Acuña et al. 2015; Dumroese et al. 2015).

Seed zones for important commercial forest trees in the United States and Canada are based to some degree on genetic testing using common garden studies and various methodological approaches to delineate seed zones or breeding regions of similarly adapted genotypes (Ying and Yanchuk 2006; Hamann et al. 2011). An alternative approach to manage seed movement is to indicate a maximum climatic or geographic transfer distance between the seed origin and the planting site (Rehfeldt 1988; Parker 1992; Lesser and Parker 2006). Ideally, both delineation of locally adapted populations and population transfer guidelines are based on knowledge from reciprocal provenance trial series that test genotypes over multiple environments (Taïbi et al. 2014; Benito-Garzón and Fernández-Manjarrés 2015). Such data, however, are only available for a few important tree species, and typically only for the portions of their natural range where commercial forestry operations take place.

For all other species, where only a few genecology studies or provenance trials are available to estimate genetic population differentiation, or where long-term field trials are lacking, reforestation is guided by proxy information (Potter and Hargrove 2012). Because forest trees are normally adapted to landscape-scale climatic and physiogeographic features, seed zone delineations are often first drawn based on ecosystem delineations or

⁵ Instituto de Investigaciones Agropecuarias y Forestales, Universidad Michoacana de San Nicolás de Hidalgo (IIAF-UMSNH), Av. San Juanito Itzicuaru s/n, Col. Nueva Esperanza, 58330 Morelia, Michoacán, Mexico

⁶ Facultad de Biología, UMSNH, Ciudad Universitaria, Avenida Francisco J. Múgica s/n, 58030 Morelia, Michoacán, Mexico

administrative boundaries, and later refined as genetic information from long-term provenance trials becomes available (Morgenstern 1996; Ying and Yanchuk 2006). More recently, provisional seed zones have been based on macro-climatic regions rather than ecosystem delineations (Potter and Hargrove 2012). The rationale for this change is that climatic regions can be re-drawn under observed and projected climate change to match genotypes to new environmental conditions. Examples of climate-based seed zones include delineations that largely reflect climatic gradients in minimum temperature and precipitation for the United States (Bower et al. 2014), minimum temperatures in Canada, where this climate aspect is of overwhelming importance (McKenney et al. 2001), or multivariate techniques that translate ecosystem delineations to climatic zones (Gray and Hamann 2011; Potter and Hargrove 2012).

In Mexico, there are still few long term common garden experiments for a limited number of species that would allow the delineation of individual seed zones (e.g. Hernández-Martínez et al. 2007; Hodge and Dvorak 2014), and current seed zones are largely based on physiographic provinces and sub-provinces (CONAFOR 2014). Seeds are normally collected in natural stands (seed orchards in general are not available) and deployed in most cases within the natural range of the species although not necessarily within the same seed zone. In some cases, planting stock production is based on seed collections in adjacent zones because seed production facilities are limited even for the main tree species. Although physiographic provinces and sub-provinces reflect climatic gradients to some degree, the current zonation (CONAFOR 2014) may include large climatic differences in elevation even within the finest classification.

Here, we propose an alternative climate-based provisional seed zone delineation for Mexico, based on overlapping GIS layers of minimum temperature and an aridity index, similar to a zonation developed for native plants in the United States (Bower et al. 2014). Taking advantage of the capability of climate-based seed zones to be re-drawn under climate change scenarios, we evaluate the changes in the spatial extent of these zones under climate change observed over the last three decades as well as under climate change projections for the 2050s, aiming to provide foresters with a perspective of how seed source and planting regions have already shifted with respect to their climate conditions, and may further shift in the medium-term future in a forestry planning context.

Methods

We followed the methodology of Bower et al. (2014) to delineate seed zones as areas of similar climate based on mean coldest month temperature (MCMT) and annual heat-moisture index (AHM), a measure of aridity that is calculated as $(\text{mean annual temperature} + 10) / (\text{mean annual precipitation} / 1000)$ (Rehfeldt et al. 1999). Cold temperature tends to be an important driver of genetic differentiation even in sub-tropical regions (Morgenstern 1996; Sáenz-Romero and Tapia-Olivares 2008; Loya-Rebollar et al 2013; Gapare et al. 2015), and Mexico's main forestry regions in the Sierra Madre and the Volcanic Belt regions experience frost conditions in the winter months. Annual heat:moisture index is indicative of evapotranspirative demand, a variable that governs tree growth under limited moisture conditions. Temperature and water availability are often largely independent, i.e., for many landscapes we have all combinations of dry/wet and cool/warm climates. In combination, minimum temperatures and water availability have proven useful to explain

both the genetic differentiation among trees populations and the phenotypic plasticity of tree populations in response to climate (Sáenz-Romero et al. 2017).

For climatic characterization that largely precedes anthropogenic climate change, we used a reference period (the 1961–1990 climate normal) to represent climate to which forest tree populations are putatively adapted. The period was chosen because it largely before a strong anthropogenic warming signal and has good weather station coverage. We use intervals of 3 °C for MCMT and intervals of AHM that are approximately equal width under a log-transformation, rounded to the nearest unit of five, and open-ended for the highest and lowest values. An approximate log-scaling is useful for variables related to water availability that have a skewed distributions, so that not too many intervals are used to classify a very small portion of the study area. We should note that depending on the size of the study area, one may choose larger or smaller intervals. This would not qualitatively influence the results of climate region shifts. For Mexico, the intervals we selected allow for a good visualization of climate regions at the full scale of the study area as well as for more local visualizations. In total, we have ten classes of MCMT that were intersected with seven classes of AHM to represent 70 potential seed zones for Mexico. The data for these climate variables for Mexico was obtained from interpolated climate data for North America (Wang et al. 2016) that is publicly available (<http://tinyurl.com/ClimateNA>).

We repeated the zoning process, using the same MCMT and AHM interval values, but using as input climate projections for the 2041–2070 period (hereafter referred to as 2050s), using an average ensemble projection across 15 CMIP5 models (CanESM2, ACCESS1.0, IPSL-CM5A-MR, MIROC5, MPI-ESM-LR, CCSM4, HadGEM2-ES, CNRM-CM5, CSIRO Mk 3.6, GFDL-CM3, INM-CM4, MRI-CGCM3, MIROC-ESM, CESM1-CAM5, GISS-E2R). The models were implemented under two Representative Concentration Pathways (RCP) of radiative forcing due to greenhouse gases: 4.5 W/m² (resulting in approximately 2 °C warming in global temperature by the end of the century) and 8.5 W/m² (approximately 4 °C warming). The projected climate data are based on the delta method, overlaying an ensemble of CMIP5 climate change projections for the 2050s on the high-resolution 1961–1990 reference period, described in detail by Wang et al. (2016), also publicly available (<http://tinyurl.com/ClimateNA>).

To show the climate change over the last approximately 30 years, we calculate the difference between the 1961–1990 normal reference period and an average climate for the 1991–2015 (25 years, rather than a 30 years normal period). We used the updated CRU-TS 3.22 dataset (Harris et al. 2014) originally developed by Mitchell and Jones (2005), to calculate a medium spatial resolution (0.5°) anomaly layer between the two periods, which was subsequently overlaid on the high resolution 1961–1990 reference layers described above, using the delta method as well. The mid-point of the two periods are 1975 and 2003, thus it represents 28 years of observed climate change. Our chosen future projection (2050s) represents another approximately 50 years of climate warming relative to the midpoint of the 1991–2015 period.

We overlaid the CONAFOR (2014) regions and subregions and the Level III ecoregions of Omernik and Griffith (2014). The comparison with CONAFOR regions and subregions allows us to evaluate differences to the current approach to guiding seed movement in México's reforestation programs, and to make recommendations how the climate-based seed transfer might complement the current system. The comparison with the Level III ecoregion classification system allows us to evaluate the ecological relevance of the climate variables that we have chosen for our climate-based seed zone delineations.

Results and discussion

Climate-based seed zone delineations

Maps of mean coldest month temperature (MCMT) and annual heat moisture index (AHM) show relatively independent geographic distributions throughout Mexico (Fig. 1). MCMT primarily reflects elevational gradients with warm areas on the coasts and colder areas in the mountains along the Mexican Trans-Volcanic Belt, the Sierra Madre Oriental, and the Sierra Madre Occidental, as well as in the high elevation deserts of the Central-Northwest Plateau in northern Mexico. In contrast, AHM intervals exhibit more complex patterns. Lower elevation areas in the southern areas have low AHM values. Although temperatures are high, high precipitation throughout the year results in an evapotranspiration surplus. The highest moisture surplus occurs on the leeward side of the Sierra Madre Oriental, facing the Gulf of Mexico. Other mountain ranges also show low AHM values with adequate moisture and lower temperatures. High AHM values with an evapotranspiration deficit, on the other hand, are found at low elevation areas around the Gulf of California and in the central and northern interior plateaus of Mexico in the rainshadow of the Sierra Madre Occidental (Fig. 1).

The overlay of the MCMT and AHM classification bands resulted in 63 seed zones in Mexico (of a potential of 70 zones) (Fig. 2). Of those, 32 bands are present on at least 1% of the total land area (color codes highlighted with bold rectangles in the legend of Fig. 2). Most of the small or missing zones belong to the extreme ranges of environmental conditions (very cold or very dry), and have been omitted from the legend for Fig. 2.

A visual comparison of climate-based zones and ecological zones shows a fairly high correspondence. For example, in Panel A of Fig. 2, dark blue colors coincide with the conifer forests dominated by *Abies religiosa* (a high altitude conifer) in the Monarch Butterfly Biosphere Reserve (Ramírez et al. 2003; Tucker 2004; Sáenz-Romero et al. 2012). Panel B of Fig. 2 accurately reflects the ecosystem transitions from the high altitude conifer forest on the Sierra Madre Oriental (dark blue) and the pine-oak forest of the Sierra Norte of Oaxaca (dark green and light blue) to the humid, warm tropical areas on slopes facing the Gulf of Mexico (orange and reddish colors) (Castellanos-Bolaños et al. 2010;

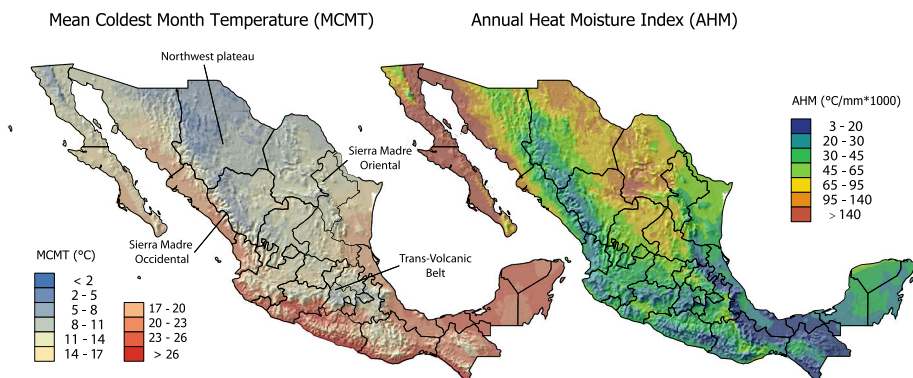


Fig. 1 Mean coldest month temperature (MCMT) and annual heat moisture index (AHM) bands. The 10 MCMT bands correspond to 3 °C intervals (except for those containing lowest and upper extreme values). AHM was calculated as mean annual temperature (MAT, °C) plus 10 °C (to obtain positive values) divided by mean annual precipitation in meters

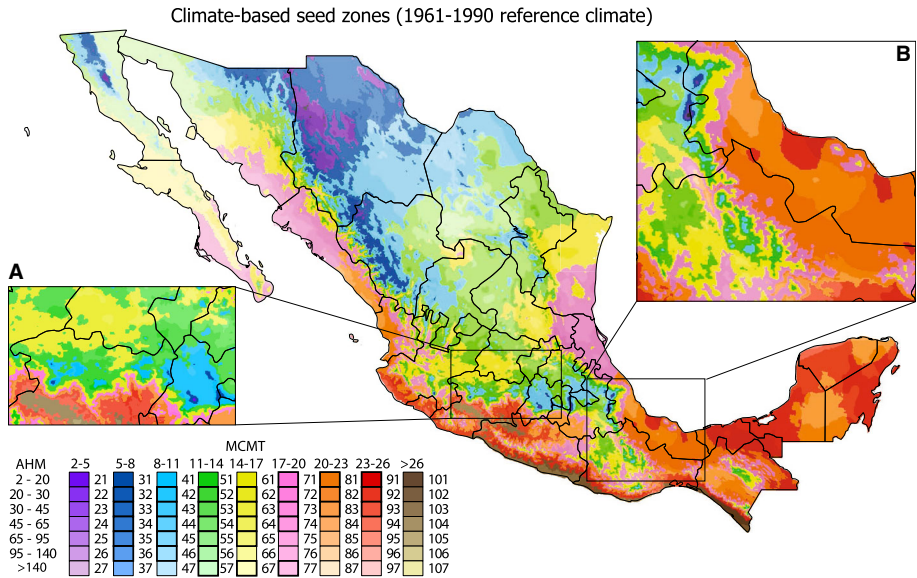


Fig. 2 Proposed climate-based seed zones for México, based on intervals of the variable mean temperature of the coldest month (columns in the legend) and on seven aridity index intervals (rows). Boxes with thick lines in the color legend are seed zones that represent at least 1% of the land area. The first column of the legend (MCMT of -1 to 2 °C) was omitted. Lines indicate state boundaries. (Color figure online)

Sáenz-Romero et al. 2010; Zacarías-Eslava and Castillo 2010). In the northwestern portion of the country, purple and blue colors, accurately represent coniferous forests where (at the border between Chihuahua and Durango states) spruce occurs (Ledig et al. 2000, 2010).

Comparison to ecoregions and CONAFOR seed zones

A comparison with Omernik's Level III ecoregions shows relatively high correspondence to our climate-based zones, indicating that our two-variable method of climate region

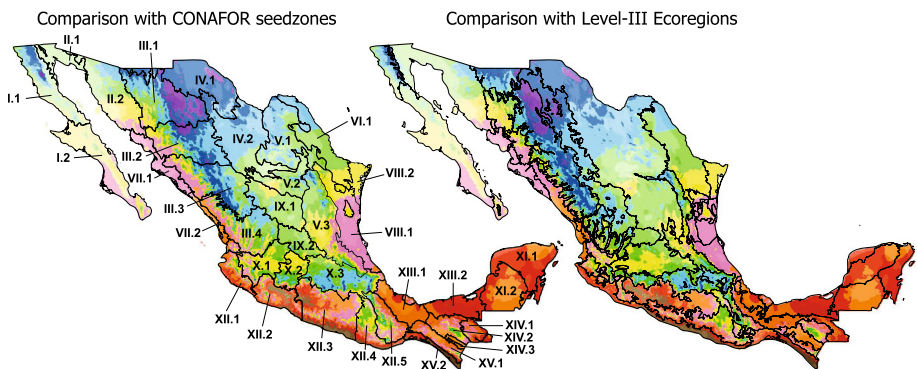


Fig. 3 Comparison of CONAFOR regions (left) and Level-III Ecoregions by Omernik and Griffith (right), both indicated by black lines, with the proposed climate-based seed zones for the 1961–1990 climate reference period (indicated by colors as in Fig. 2)

delineation produces zones that are ecologically relevant (Fig. 3). In areas of low topographic complexity the CONAFOR seed zones also track climatic regions reasonably well, e.g. pink and red areas along the coasts (Fig. 3). However, it appears that CONAFOR subregions are too coarse for areas with high topographic complexity that include high climatic variation related to elevation gradients, as for example CONAFOR zones III.1, III.2 and III.3, that are crossed by Sierra Madre Occidental. To decrease the risks of an excessive seed movement inside each zone, seed transfer rules for CONAFOR seed zones included a restricted altitudinal movement from the seed source to planting site of no more than 300 m upwards or 150 m downwards to ensure adapted plantations.

Elevation is considered in the delineation of Level III ecoregions (Omernik and Griffith 2014); thus, Level III ecoregions shows a high degree of similarity to our climate-based zones (Fig. 3). Level III ecoregions could be used as a proxy to our climate-based seed zones for the purpose of collection of seed and deployment of planting stock without additional transfer-rules within seed zones. However, this requires the assumption of constant climate conditions. In other words, the existing zonation systems (CONAFOR and Ecoregions) are not amenable to assisted migration. Climate-based delineations such as those developed in this study allow seed zones to be redrawn using observed climate change and under future climate change projections.

Seed zone shifts under climate change

Mean annual temperature in Mexico has increased 0.66 °C over the last three decades according to our analysis, an estimate consistent with previous analyses (Pavia et al. 2009; Cuervo-Robayo 2014). Estimates for changes in precipitation are more variable among regions. Areas facing the Gulf of Mexico have seen increases in precipitation, while the west coast has seen decreases. Current reforestation programs do not have a mechanism to address these changes. The general approach of these programs is to collect seeds from a given seed zone, produce seedlings in a nursery, and reforest sites within the same zone. Current Mexican rules require that seed sources and planting sites are within the same CONAFOR seed zone. Matching seed sources with new environmental conditions under projected climate change will require a modified approach. Seedlings should be deployed in the same climate-based zone, but they would be re-mapped to account for observed climate change or future climate change projections (Fig. 4). In other words, assisted migration could be implemented by collecting seed in current procurement areas (delineated under 1961–1990 climate), and then deploying seedlings in the same climate-based zones although delineated under observed climate trends (1991–2015 climate) or under projected future climate (2050s climate).

With respect to the two variables used for climate-based seed zone delineation, we find that mean coldest month temperature (MCMT) has increased 0.74 °C over the last three decades. For annual heat moisture (AHM), we observe an average + 0.09 band shift toward drier conditions across Mexico, where bands refer to AHM intervals shown in Figs. 1 and 2. For projections for the 2050s, MCMT is predicted to increase by 1.7 °C relative to 1961–1990 reference period, and AHM is predicted to shift by + 0.23 intervals for RCP 4.5 projections. For the more pessimistic RCP 8.5 projections, MCMT is predicted to increase by 2.4 °C and AHM is expected to shift 0.33 intervals toward drier conditions, relative to the 1961–1990 reference climate period.

Observed climate change for MCMT over the last three decades (from the mid-point of the 1961–1990 to the mid-point of the 1991–2015 average) represents approximately 44% of the expected climate change by the 2050s for the RCP 4.5 scenario and 31% of the RCP

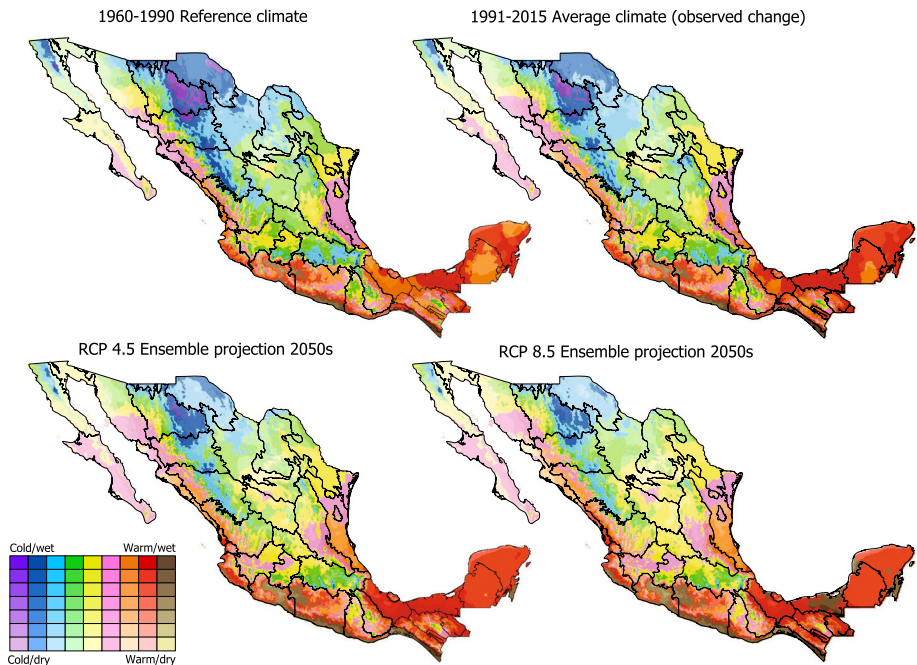


Fig. 4 Shift of climatic seedzones under observed and predicted climate change. The CONAFOR regions, indicated by black lines, are included as a reference. The 1991–2015 observed climate average is the result of climate change observed over the last three decades. The bottom row shows climate seed zone shifts for the 2050s under a moderate greenhouse gas forcing scenario (RCP 4.5), and a more pessimistic greenhouse gas emission scenario (RCP 8.5)

8.5 scenario relative to the 1961–1990 baseline. Similarly, observed changes in AHM are already equivalent to 39% of the 2050s climate projections. The consistency of the observed trend with future projections suggests that managers should already be moving populations. Collecting seed from locations that are currently warmer and/or drier and moving it to historically cooler and/or wetter climates, would compensate for climate change that has already occurred and is predicted to continue in the future. Such prescriptions may be guided by maps or tables describing regional seed zone shifts (Fig. 4, Table 1). Maps of observed change as well as projections show an increase of warmer and drier areas at the expense of colder and more humid areas. In particular, the reduction or disappearance of mountain-top climatic regions can already be observed for the recent time period 1991–2015 compared to the past (Fig. 4, loss of dark purple and dark blue regions). An increase in yellow and light blue areas representing the increase of dry and warm conditions across the interior plateau is only moderate for the observed climate but much more prevalent for both 2050s projections.

Changes have not occurred uniformly throughout Mexico. Table 1 shows the percent of the land area that has changed to a class of lower or higher for MCMT or AHM for each CONAFOR region. In terms of dryness, CONAFOR regions III, IV, and VI located in the east-facing slopes of the Sierra Occidental and the northern interior plateau show the highest increase in aridity (Table 1, column AHM + 1). In contrast, the southern CONAFOR regions VIII, XI, and XII see overall more moist conditions (Table 1, column AHM – 1), due to an increase in the intensity of hurricanes (Kang and Elsner 2015).

Table 1 Change in climate bands as defined in Fig. 2 for mean coldest month temperature (MCMT) and annual heat moisture index (AHM)

CONAFOR	Change of intervals 2000s (observed)					Change of intervals 2050s (rcp4.5)				Change of intervals 2050s (rcp8.5)			
	AHM			MCMT		AHM		MCMT		AHM		MCMT	
	– 1	0	1	0	1	0	1	0	1	0	1	0	1
I	1	92	7	59	40	96	4	35	65	89	11	13	87
II	0	82	18	70	30	89	11	28	72	77	23	4	96
III	0	76	24	68	32	73	27	34	66	54	46	6	94
IV	0	80	20	74	26	74	26	25	75	64	36	2	98
V	4	85	11	74	23	77	23	33	67	70	30	7	93
VI	0	71	29	42	58	83	17	31	69	74	26	5	95
VII	0	85	14	64	35	85	14	46	54	74	26	4	96
VIII	11	87	2	72	28	82	18	36	64	75	25	12	88
IX	0	92	8	89	9	72	28	35	65	63	37	6	94
X	1	87	12	86	14	70	30	35	65	62	38	10	90
XI	12	87	0	70	30	65	35	59	41	58	42	50	50
XII	9	88	3	90	10	76	24	41	59	69	31	21	79
XIII	5	95	0	71	29	76	24	50	50	69	31	21	79
XIV	5	95	0	62	38	87	13	37	63	87	13	19	81
XV	7	91	1	69	31	81	19	39	61	79	21	28	75

The values represent the proportion (%) of the area in each seed zone that has changed to a warmer (1) interval or has remained the same (0). Similarly, changes to AHM are indicated towards a wetter (– 1) or drier (1) interval (also visualized in Fig. 4). Columns with very low percentage values were omitted

Observed warming trends are less regionalized. All CONAFOR regions show a moderate change in their area to a class with higher MCMT values (Table 1, MCMT+1). Future projections also show less regionally pronounced differences. For the RCP 4.5 and RCP 8.5 ensemble projection for the 2050s, all CONAFOR regions will experience some level of change towards a class of higher MCMT or AHM values.

Applications and recommendations

Given the concordance of observed and projected climate change towards warmer and drier conditions, we propose that the movement of locally adapted seeds and seedlings towards colder and wetter environments than their origins would be justified and in fact likely required to ensure good survival and growth of the deployed seedlings on the coming decades (Aitken et al. 2008; Dumroese et al. 2015; Potter et al. 2017). For the climate variables used in this study, we have already experienced approximately 37% of the climate change (over three decades) that is on average projected for the 2050s (over eight decades) relative to the 1961–1990 reference period. Thus, the rate of observed climate change over 30 years is almost exactly the proportion of change that would be expected based on 2050s projections, namely 0.25 °C per decade. Given the long growing period of tree plantations, it seems prudent to start moving seed sources to compensate for climate change that has already occurred.

Current CONAFOR seed zones are meant to ensure adaptation of planting stock by preventing seed movement across climates that are too dissimilar. However, current guidelines allow some flexibility for forest managers to address observed and projected climate change by implementing the climate-based seed zones we propose here. For example, seed sources for planting in the projected light blue climate region in the northern section of seed zone VI.1 (Fig. 5a, right panel) could come from the corresponding light blue regions further south within the same seed zone under reference climate conditions (Fig. 5a, left panel). Similarly, seed sources for planting in the yellow areas in seed zone X.3 under projected climate (Fig. 5b, right panel) could be sourced from populations in the climatically corresponding yellow regions from the adjacent X.2 region current conditions (Fig. 5b, left panel). Such seed movements would compensate for the change from contemporary colder and moister green areas to dryer and warmer yellow areas by the 2050s in seed zone X.3 (Fig. 5b, left versus right panel).

Implementing seed movement based on any zone-based system, such as the CONAFOR seed zones or our climate-based seed zones, has some fundamental limitations. Zones delineated across a continuum of climate conditions or a continuum of a genetic variation should not be interpreted as distinct climate types or genetically distinct populations. Rather, the purpose of the maps we provide is to visualize where climate regions to which trees are putatively adapted have been in the past, and are predicted to be in the future. For the practitioner, they provide general guidance where seed of any species may be sourced by tracking their historic climate niche without the need of more complex focal-point seed transfer systems (e.g. Parker 1992). Note that we do not recommend that a class change alone be used as decision criterion whether seed movement is required or not. To expand

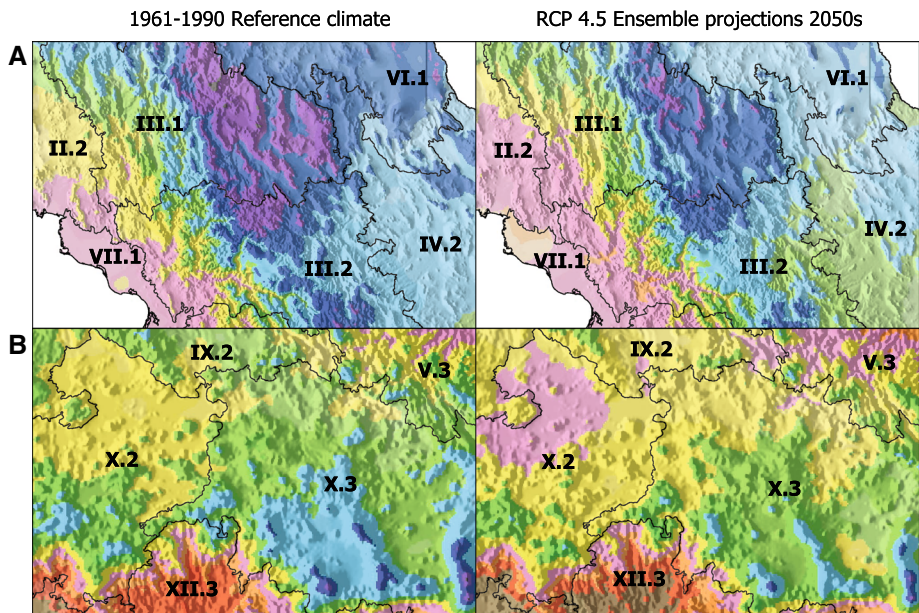


Fig. 5 Detail of climate-based seed zone shifts within CONAFOR regions, indicated by black lines. Practitioners should often be able to collect seed within the same seedzone that is predicted to become suitably adapted. For example, light blue collections in seed zone VI.1 (a, left) could be used further north in the same seedzone under predicted climate change (a, right)

on the previous example for seedzone X.3 in Fig. 5b: For a planting site in the green climate zone, close to the boundary to the warmer yellow zone (bottom right panel 2050s climate), the maps would suggest that no seed transfer is required (i.e. the site did not change from being green in the 1961–1990 left panel). However, the correct prescription would be to transfer seed from a source location close to the yellow/green boundary in the 1961–1990 reference map, the climate to which populations are putatively adapted.

Given the amount of observed and projected climate change, a simple and practical interim rule that also conforms to current Mexican legislation would be to move seeds one half of the seed zone intervals used here towards adjacent wetter and/or cooler climate-based seed zones, preferably within the same CONAFOR seed zone. This can be implemented based on the climate-based seed zones delineated in Fig. 2, whose GIS files are available through an open access database (<https://doi.org/10.5281/zenodo.1052141>). While this cannot fully address the anticipated climate shifts shown in Fig. 4, it would be a practical first step in the right direction, compensating for a general trend toward classes with a lower moisture index and higher temperatures. Such a first step would still comply with current legislation and significantly improve on status-quo management practices. Our proposed approach to track climate conditions to which organisms are putatively adapted could be refined with information on climatic tolerances from provenance testing. For species and populations with narrow climate tolerances it will be more important to track their optimum niche closely.

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