

Seasonal microclimatic variation in a succession gradient of low thorn forest in Northeastern Mexico

Uriel Jeshua Sánchez-Reyes¹, Santiago Niño-Maldonado², Ludivina Barrientos-Lozano^{1*}, Jacinto Treviño-Carreón² & Pedro Almaguer-Sierra¹

- Tecnológico Nacional de México-Instituto Tecnológico de Ciudad Victoria. Boulevard Emilio Portes Gil No. 1301. Ciudad Victoria, Tamaulipas, México. C.P. 87010; uriel elf3@hotmail.com, ludivinab@yahoo.com, almagavetec@hotmail.com
- Universidad Autónoma de Tamaulipas-Facultad de Ingeniería y Ciencias. Centro Universitario Victoria. Adolfo López Mateos, Ciudad Victoria, Tamaulipas, México. C.P. 87149; coliopteranino@hotmail.com, jatrevino@docentes.uat.edu.mx * Correspondence

Received 05-VI-2018. Corrected 16-VIII-2018. Accepted 27-XI-2018.

Abstract: Global increase in land cover change and deforestation bring about fragmentation of a high proportion of native vegetation areas. Microclimate is among the first modified factors after vegetation loss, effects of such disturbances are critical for species performance. However, both secondary succession and seasonality provoke further modifications in abiotic environment after disturbances. Although microclimate patterns during succession are well studied for several ecosystems, they are practically unknown for low thorn forests. In Northern Mexico, this is an endangered ecosystem characterized by harboring a high percentage of endemics. Measurement of microclimatic factors is crucial for understanding possible consequences of post-disturbance time on species inhabiting this ecosystem. This work aimed to assess seasonal variation of microclimatic patterns in a succession gradient of four categories (conserved areas, 31, 17 and four years of succession). The study area was delimited using Landsat satellite images (1973, 1986, 2000, 2005, and 2013) in a fragment of low thorn forest in Northeastern Mexico. For microclimate characterization we studied wind speed, temperature, relative humidity, heat index, dew point, and evapotranspiration. Variables were measured monthly on eight plots, in each of the four successional categories, during two different seasons: wet (May through October 2016) and dry season (November 2016 through April 2017). A multivariate discriminant function analysis showed that microclimate differs among successional stages. In the wet season, early succession areas were characterized by higher values of heat index and wind speed, contrary to conserved areas. In the dry season, successional differences were attributed to wind speed and relative humidity. Moreover, microclimate differences between categories and importance of variables measured were both higher only during the dry season. Our results show that seasonality influences greatly microclimatic patterns during secondary succession. In addition, each one of the successional categories exhibited unique microclimatic conditions. Remarkably, four, 17, and even 31 years succession categories differed from conserved areas. This work provides evidence on the great relevance of seasonality and microclimate for studying secondary succession. It is suggested to take both factors into consideration when implementing conservation programs concerning endangered habitats such as low thorn forests. As an ecosystem poorly studied, microclimate characterization provided herein, shall help to a better understanding and management of these areas.

Key words: disturbance; secondary succession; chronosequence; abiotic factors; seasonality; geographic information systems.

Sánchez-Reyes, U. J., Niño-Maldonado, S., Barrientos-Lozano, L., Treviño-Carreón, J. & Almaguer-Sierra, P. (2019). Seasonal microclimatic variation in a succession gradient of low thorn forest in Northeastern Mexico. *Revista de Biología Tropical*, 67(1), 266-277.

•

266

Land use and cover change are among major factors that produce loss of biodiversity worldwide (Foley et al., 2005). Fragmentation of a high proportion of native areas is increasing, recent studies document a global deforestation of 2.3 million square kilometers (Hansen et al., 2013). Therefore, the current landscape is made up mostly by patches of conserved vegetation and secondary vegetation areas (Aide et al., 2012; Hansen et al., 2013; Ferraz et al., 2014; Frey et al., 2016) of different degree and time of disturbance (Melo, Arroyo-Rodríguez, Fahrig, Martínez-Ramos, & Tabarelli, 2013). These changes in land cover influence ecological processes and pose important consequences for species (Foley et al., 2005) and biotic communities (Parr, 2012).

Microclimate is one of the factors that changes first after loss of vegetation (Norris, Hobson, & Ibisch, 2012; Parr, 2012; Hardwick et al., 2015). Disturbance augments the incidence of light, air temperature and wind velocity, and decreases the relative humidity and humidity in both soil and litter (Guariguata & Ostertag, 2001; Swanson et al., 2011; Frey et al., 2016). Secondary succession, on the other hand, involves the modification of plant communities after a disturbance event (Pickett, Cadenasso, & Meiners, 2008; Pulsford, Lindenmayer, & Driscoll, 2016). Thus, the increase in leaf area values and complexity of canopy structure in mature areas favor higher humidity and lower temperatures (Guariguata & Ostertag, 2001). Such microclimatic conditions are determinant for the presence and establishment of species during the succession (Arroyo-Rodríguez et al., 2017), additionally, ecological responses of species to these successional modifications are different (Swanson et al., 2011). Therefore, analysis of microclimatic fluctuations caused by disturbance and subsequent recovery of vegetation, are necessary to understand the dynamics of biodiversity in secondary forests (Frey et al., 2016).

The use of chronosequences for the study of succession has been conducted mostly in tropical rainforests (Guariguata & Ostertag, 2001; Breugel, Martínez-Ramos, & Bongers, 2006), and in seasonal dry tropical forests (Lohbeck et al., 2014; Craven, Hall, Berlyn, Ashton, & Breugel, 2015). However, there are few studies in which the dynamics of microclimate is exclusively analyzed during succession (Lebrija-Trejos, Pérez-García, Meave, Poorter, & Bongers, 2011), these changes have not been monitored in other vegetation types, such as low thorn forests in Northeastern Mexico. These vegetal communities constitute fragmented and threatened areas of great biological importance, with a high number of endemic plants and species richness (García-Morales et al., 2014; Sánchez-Reyes, Niño-Maldonado, Barrientos-Lozano, & Treviño-Carreón, 2017). Therefore, it is crucial to understand the possible consequences of disturbance and succession on interactions between microclimate and species in those areas, so that conservation strategies can be efficiently applied.

An important feature of low thorn forests is its climate regime, since they can be considered as dry tropical forests or deciduous tropical forests according to their precipitation range (Challenger & Soberón, 2008; Trejo, 2010), although their seasonality is not as strong as that observed in dry forests of the Mexican Pacific (Ceballos et al., 2010). In this sense, there is evidence that climate variation associated with seasonality of an area also influences both vegetation recovery processes (Bernhardt-Römermann et al., 2011) and microclimate of secondary forests (Grimmond et al., 2000). This is because the conditions of forested areas (compared to open or disturbed areas) show lower seasonal variability (Ewers & Banks-Leite, 2013; Kovács, Tinya, & Ódor, 2017). In addition, it has been observed that seasonality changes significantly abiotic gradients during vegetation recovery in tropical dry forests. This is originated by higher microclimatic heterogeneity in the wet season than in the dry season (Lebrija-Trejos et al., 2011). In summary, early succession is commonly characterized by higher temperature and lower humidity (in contrast to conserved areas), and low thorn forest can be categorized within the dry forests (Challenger & Soberón, 2008; Ceballos et al., 2010;

Trejo, 2010); accordingly, we hypothesize that differences between succession categories will be higher in the wet season than in the dry season. Based on the above, the study aimed to: a) quantify microclimatic variation in areas of low thorn forest with different time of succession, and b) determine how these patterns change according to seasonality.

MATERIALS AND METHODS

Study area: This work was carried out from May 2016 to April 2017. The study area is located northwest of the municipality of Victoria, in the state of Tamaulipas, Northeastern Mexico. Succession gradient was delimited on a small homogeneous plain of approximately 400 ha (4 km²), at 320-350 masl with East exposure. The area is set between the skirts of the Sierra Madre Oriental (SMO) and rural areas of Ejido (Ej.) Rancho Nuevo and Ej. Santa Ana (23°51'00" - 23°51'45" N & 99°13'15" -99°14'00" W). Dominant vegetation type in the studied fragment is low thorn forest (INEGI, 2013), although it shares elements with submontane scrub and Tamaulipan thorn scrub communities (García-Morales et al., 2014) in areas of secondary vegetation. Low thorn forest in the study area can be designated as deciduous (INEGI, 2013) or semideciduous (Treviño-Carreón & Valiente-Banuet, 2005). It is characterized by thorny tree species, 8 to 10 m height, and a high proportion of species (50 to 75 %) that loses their leaves during the dry season (Treviño-Carreón & Valiente-Banuet, 2005). Climate in the area is warm subhumid with summer rains. Annual average temperature ranges from 18 to 24.3 °C, and total annual precipitation fluctuates between 717.3 to 1 058.8 mm (Almaguer-Sierra, 2005); however, long drought periods are a common pattern during several months.

Successional gradient: The succession gradient was delimited based on the processing, classification and analysis of Landsat satellite images of years 1973, 1986, 2000, 2005 and 2013, which were obtained from the Global

Land Cover Facility (GLCF-GLS, 2016) and USGS Global Visualization Viewer (GLOVIS, 2016) websites. Each of the four last images had a spatial resolution of 30 m; thus, it was necessary to modify the cell size of the 1973 image, from 60 to 30 m. We followed a method for delimiting approximate time for chronosequences and successional time using satellite imagery (Sánchez-Reyes et al., 2017), which is briefly described here. First, images were automatically segmented. Then, some segments were manually selected as training fields, from which a spectral signature was extracted to classify the images into each of the following four land cover categories: conserved low thorn forest, secondary low thorn forest, modified areas, and bare soil areas; such classification was done by using the maximum likelihood algorithm. Through a reclassification, the four land cover categories were merged as follows: vegetation (conserved and secondary low thorn forest), and disturbance (modified and bare soil areas). Using these two simplified categories, images were processed by cross tabulation to designate the final successional categories for this study. 1) Conserved areas. Closed canopy: trees with heights up to 15 m, diameters at breast height (DBH) up to 50 cm; an heterogeneous number of shrubs and herbaceous plants; species such as Celtis pallida Torr., Casimiroa greggi (S. Watson) F. Chiang, Ebenopsis ebano (Berland.) Barneby & J. W. Grimes, and Mascagnia macroptera (DC.) Nied. 2) Areas with 31 years of succession. Closed canopy: trees up to 9 m height, DBH up to 25 cm; a low number of herbaceous plants, but a contrastingly higher number of shrubs; species such as Havardia pallens (Benth.) Britton & Rose, Randia obcordata S. Watson, Cordia boissieri A. DC., and Croton cortesianus Kunth. 3) Areas with 17 years of succession. Open to closed canopy: trees up to 7 m height, DBH up to 18 cm; a high number of shrubs and herbaceous plants; species such as Acacia farnesiana (L.) Willd., H. pallens, Mimosa malacophylla A. Gray, and Sida acuta Burm. 4) Areas with four years of succession. Open areas: absence of trees, dominance of shrubs from 1 up to 2.5 m height, and

an homogenous herbaceous cover on the forest floor; species such as *Calyptocarpus vialis* Less., *C. cortesianus, Malvastrum coromandelianum* (L.) Garcke, *M. malacophylla*, and *Solanum erianthum* D. Don. Characterization of each category was done on basis of identification and visual observation of vegetation. The study area historical disturbance is characterized by slash and burn for conversion to agriculture areas, which was corroborated by interviewing owners of local farms; therefore, original type of disturbance was the same for all areas. Procedures were conducted with the aid of IDRISI Selva 17.0.

Microclimate measurement: Eight plots of 10 x 10 m in each of the four successional categories were delimited randomly using Geographic Information Systems (GIS) software (Digital appendix 1). Successional categories consisted of several patches of different forms and areas; thus, for a random distribution of plots, all patches within each category were unified. Although we had several replicates of categories, the random procedure originated an unequal number of plots by patch (Digital appendix 1). Therefore, we considered plots as the replicates of successional categories, since through the used procedure these plots were randomly located. Besides, their independence was guaranteed by locating each plot with a minimum distance of 40 m from other plots or successional categories, in order to avoid edge effect and influence of surrounding microclimate (Davies-Colley, Payne, & Elswijk, 2000; Gehlhausen, Schwartz, & Augspurger, 2000). Subsequently, microclimate measurements were performed monthly from May 2016 through April 2017 on each plot. Variables measured are as follows: 1) wind speed, 2) temperature, 3) relative humidity, 4) heat index, 5) dew point, 6) evapotranspiration. Heat index as considered here measures thermal stress or thermal sensation by combining temperature and humidity (Anderson, Bell, & Peng, 2013; Lee & Brenner, 2015); as such, it has not been considered as a microclimatic variable for successional analysis, but recent studies show its

association with species distribution (Sánchez-Reyes, Niño-Maldonado, Barrientos-Lozano, Jones, & Sandoval-Becerra, 2015; Sandoval-Becerra et al., 2017). Microclimatic variables were recorded at the center of each plot using a Kestrel 4500 portable weather station, which was placed 1.5 m above the ground, attached to a metal pole, bearing a protection at the top to avoid direct solar radiation. The device was programmed to record variable measurements every 30 min for 12 h (06:00-18:00 h). Three weather stations were placed simultaneously, each one in a different plot. After recording measurements, the devices were transferred to the next three plots, until the 32 plots were evaluated. Therefore, variable measurements required 11 consecutive days monthly, that is, each plot had only one measurement by month. All measurements were conducted in clear or partly cloudy days, with no precipitation.

To assess the influence of seasonality on microclimate variation along the successional gradient, variables measured were analyzed taking into account two major seasons that characterize the study area (Secretaría de Gobierno, 2015). Wet season, from May through October 2016, and dry season from November-2016 through April-2017; i.e., six months each season. For each microclimate variable, we calculated the average monthly value at each plot (the average value of measurements from 12 hours). These values were used to estimate statistically significant differences between succession categories, applying a discriminant function analysis (FD). Data were analyzed separately for the wet and the dry seasons. This method aims to find those factors that contribute most to separate the groups, by searching for the best linear combination of the original variables, which originates new variables known as discriminant functions or roots. Interpretation was accomplished taking into account the first two significant roots of the analysis, which represent the best discrimination between groups (Rencher, 2002). The Wilk's Lambda value obtained, is a measure of the deviations within each group with respect to the total deviations. It assumes values between

0 and 1. Values close to 0 indicate a high discriminant capacity of the variables; while values close to 1, indicate a low capacity to discriminate (Pozo-Díaz & Carrasco, 2005).

The FD analysis allowed to determine the F and p values between pairwise comparisons of categories, to test for significant differences in succession categories based on microclimatic variables. In addition, the relative contribution of each variable measured to the separation of succession categories was quantified, according to the correlation values between these variables and the new discriminant functions; these correlations are known as loadings or factor structure coefficients (Rencher, 2002).

Finally, the FD showed the optimal graphical distribution for each plot, i.e., it depicts the best discrimination of the groups/succession categories, based on its total microclimatic variation. Such observations are called canonical observations or canonical scores (James & McCulloch, 1990; Rencher, 2002; Karels, Bryant, & Hik, 2004). Also, the average canonical values of the observations in each group, or centroids, were obtained; these represented the average microclimatic conditions in each succession category. The interpretation of both graphs (scores and centroids) was made according to the variable with the highest correlation value (factor structure coefficients or loadings) for each root, since they had the greatest contribution to the separation between succession categories. Discriminant function analysis was carried out using STATISTICA 8.0 (StatSoft Inc., 2007); the graphs were generated in Arc-GIS 10.9 (Esri, 2013).

RESULTS

The discriminant function analysis indicated significant global differences between the succession categories as a function of the microclimate, both in the wet season ($F_{18, 518} = 2.7877$; P < 0.0001) and the dry season ($F_{18, 518} = 7.1442$; P < 0.0000). The discriminant value of the model was higher in the dry season (Wilks 'Lambda = 0.53414) than in the wet season (Wilks' Lambda = 0.76991).

In the wet season, both roots of FD explained similar percentages of the microclimate variation between categories, with a 51.98 % (eigenvalue = 0.14422) for the root 1, and a 42 % (eigenvalue = 0.116534) in the root 2. According to pairwise comparisons, the microclimate observed in the category of 17 years does not differ from that registered in areas with four and 31 years of succession; the remaining comparisons were significantly different (Digital appendix 2). Microclimatic variation explained by the two FD roots was higher in the dry season, since 69.70 % (eigenvalue = 0.516675) was described by root 1, and only 22.21 % (eigenvalue = 0.164619) was explained by root 2. The pairwise comparisons during the dry season indicated that the microclimate is different amongst all successional categories (Digital appendix 2).

During the wet season, in root 1, the variable with the highest correlation value was the heat index (-0.60); while in root 2, wind speed was the most important variable (-0.76) (Digital appendix 3). In the dry season, wind speed had the highest correlation value in root 1 (0.89), and relative humidity was the most important variable in root 2 (0.95), followed by temperature (-0.79) and heat index (-0.66) (Digital appendix 3). The magnitude of the correlations for the most important variables in the dry season was higher with respect to the main variables of the wet season (Digital appendix 3).

Microclimate characterization in the wet season: Distribution of canonical scores (microclimate observations in each plot) was plotted only for the most important variable on each root. The microclimatic conditions during the wet season were more homogeneous, since the separation of canonical scores as a function of the variables was not evident (Digital appendix 4). Overall, in the horizontal axis (root 1), both the conserved areas and the sites of four and 17 years of succession presented average heat index values, close to the origin of the graph. However, in conserved areas, there was a tendency towards lower values of the variable, while in categories of four and 17 years of succession plots were located in areas with higher heat index values. In areas with 31 years of succession there was also a trend towards higher values of heat index than those presented in the other categories (Digital appendix 4A). Regarding the vertical axis (root 2), the highest wind speed values were recorded in areas with four, 17 and 31 years of succession, whereas these values were significantly lower in conserved areas (Digital appendix 4B).

A more specific microclimate characterization of the succession categories was performed based on the position of the centroids; that is, according to the canonical average of the microclimatic values observed in the plots, and was also interpreted only with the two most important variables. In the wet season, differences between succession categories were more evident when analyzing the centroids (Digital appendix 5). Thus, sites with four and 17 years of succession had a heat index close to 40.7 °C, but differed in wind speed since in areas of lower succession average values ranged between 1.25 and 1.5 km/h, whereas in the category of 17 years the values were lower, between 1 and 1.25 km/h. The highest heat index value was obtained in areas with 31 years of succession and fluctuated from 42 °C to 43.29 °C, with a wind speed of 1.25 to 1.5 km/h. For both variables, the lowest values were obtained in conserved areas, with an average heat index of 38.09 °C and a wind speed between 0.25 and 0.5 km/h (Digital appendix 5).

Microclimate characterization in the dry season: Separation of canonical scores, and therefore differentiation between succession categories, was more evident in the dry season (Digital appendix 6). In the horizontal axis (root 1), early succession sites were concentrated mainly in the right end of the graph, so they had higher wind speed values; contrarily, areas of 17 and 31 years of succession were scattered towards the left quadrant, indicating lower wind speed. Most of the conserved

areas were located in the center and left of the canonical graph, displaying a low or average wind speed (Digital appendix 6A). In the vertical axis (root 2) the separation of the canonical observations was higher, and exhibited a progressive decrease of relative humidity from the conserved areas where the highest values were presented, towards the plots with four years of succession where the lowest humidity was obtained (Digital appendix 6B).

During the dry season (Digital appendix 7), the areas with four years of succession were characterized by a wind speed of 1.75 to 2.25 km/h, and a relative humidity of 60.79 to 62.2 %. Categories of 17 and 31 years presented values of wind speed below 0.25 km/h; however, relative humidity in areas of 17 years ranged from 62.2 to 63.59 %, while in the category of 31 years values were close to 65 %. Finally, most conserved areas recorded a wind speed of 0.25 to 0.5 km/h, and the highest relative humidity value, which oscillated between 66.4 and 67.8 % (Digital appendix 7).

DISCUSSION

According to the observed results, early succession areas were related to higher temperature and lower relative humidity, in contrast to areas that have acquired more vegetation cover, i.e. conserved areas. Changes in relative humidity agree with similar studies accomplished on different vegetation cover types (Hojdová, Hais, & Pokorný, 2005). However, temperature was not a significant microclimatic variable for separation of succession categories in this study, despite that the importance of this variable has been demonstrated in other chronosequences (Norris et al., 2012) and forest studies with different degree of perturbation (Hojdová et al., 2005; Hardwick et al., 2015). Instead, heat index was one of the variables that contributed most to discriminate between categories in both seasons. Aside to the results here obtained, there is no antecedent (to our knowledge) of inclusion of heat index in other microclimate analysis associated with succession. However, its importance has

been demonstrated in ecological niche studies for species of leaf beetles (Chrysomelidae) (Sánchez-Reyes et al., 2015) and disturbance gradients (Sandoval-Becerra et al., 2017). This variable measures thermal stress in humans by combining temperature and humidity, and it is frequently used to calculate the "apparent temperature", also known as thermal sensation (Anderson et al., 2013; Lee & Brenner, 2015). Therefore, differences found in the succession categories attributable to this variable, suggest a synergistic effect of humidity and temperature on the environment and consequently, on the species present in the study area.

Variation in microclimatic succession patterns is attributed mostly to the incidence of light, modified in turn by vegetation structure. In recently disturbed or early succession areas, low or absent tree cover allows higher direct solar radiation, rising air temperature and reducing humidity; over time, increase in canopy complexity reduces the incidence of light (Lienard, Florescu, & Strigul, 2015) and generates different temperature and humidity conditions (Hardwick et al., 2015). Consequently, modifications on those variables are reflected in changes in heat index. Wind speed was also an important variable in separating succession categories in this work. This variable is considered of relevance for transpiration of plants under the canopy (Renaud et al., 2010). Its variation stems from the presence of trees and vegetation (Renaud et al., 2010; Hardwick et al., 2015). As a normal pattern, wind speed decreases with the increase in complexity of vegetation structure (Hardwick et al., 2015), being consistent with the results observed in this study since plots with earliest succession time showed highest values in wind speed. The significance of this variable in our study area may be related to its influence on dispersal of plant propagules (Damschen et al., 2014; Schurr, Bond, Midgley, & Higgins, 2005), which is transcendental for the succession process. Accordingly, it is possible that higher wind values in recently disturbed areas may influence successional routes by introducing plant species characteristic of other vegetation

types. Such influence needs to be analyzed in future studies.

Seasonality is a very important factor in succession analysis, since variation in abiotic climate factors in a given area contributes to post-disturbance resilience processes (Bernhardt-Römermann et al., 2011). This work provides evidence on the influence of seasonality in microclimate along a successional gradient. During the dry season, relative humidity (RH) was related to successional differences indicating that different categories of succession may retain different RH conditions. Contrarily, as humidity is not a limiting factor in the wet season, it would be expected that other variables gain importance, as was observed with heat index. Such microclimate variations during succession are of major importance, since these abiotic constraints at a local scale are related to species distribution (Checa, Rodriguez, Willmott, & Liger, 2014). Moreover, microclimatic seasonality is determinant for the development and establishment of vegetation (Lebrija-Trejos et al., 2011).

However, although the effect of seasonality on microclimate during succession was evident in this study, results rejected our hypothesis. Significant differences amongst all succession categories were observed in the dry season, whereas in the wet season 17 years succession areas showed similar microclimate values as those of four and 31 years succession. In addition, variables correlation values were lower during the wet season than in the dry season. Other studies carried out in dry forests in Mexico have shown contrary patterns to our findings, since microclimatic heterogeneity is higher during the wet season (Lebrija-Trejos et al., 2011). These discrepancies may be attributed to minor seasonality conditions in Northeastern Mexico compared to the dry forests of the Mexican Pacific Coast (Challenger & Soberón, 2008; Ceballos et al., 2010; Trejo, 2010). This suggests a higher heterogeneity in characteristics and vegetation structure between categories, bring about by greater variation in the number of plant species and individuals that resist leaf fall during the

dry season along the succession gradient. It has been observed that leaf area has a strong effect on microclimate, and that a high leaf area index gives rise to cooler environments (Baker et al., 2014; Hardwick et al., 2015). Therefore, the increase in plant productivity and development of new leaves during the wet season may reduce microclimate variation at intermediate areas of succession, because of a more homogenous vegetation structure. Bernhardt-Römermann et al. (2011) report similar results, they found that resilience after disturbance is lower in dryer or arid areas. Accordingly, in the dry season differences between succession categories must be higher, as shown in this research.

Although vegetation type herein studied is categorized as low thorn forest (INEGI, 2013), because of its characteristics it could also be considered within the dry forest category (Challenger & Soberón, 2008; Ceballos et al., 2010; Trejo, 2010). Among the most important characteristics of these ecosystems, in contrast to similar Neotropical forests, is its strong seasonality that causes low or null precipitation during the dry season months (Ceballos et al., 2010; Trejo, 2010). Nonetheless, particular conditions in the study area, such as minor seasonality, presence of certain plant species [i.e. Ebenopsis ebano (Berland.) Barneby & J. W. Grimes or Havardia pallens (Benth.) Britton & Rose] and geographic location (Miranda & Hernández, 1963; Treviño-Carreón & Valiente-Banuet, 2005) seem to provide for the observed microclimatic variations. This may be because intensity of the gradient depends on similarity of conditions between succession stages as a function of the habitat structure (Letcher et al., 2015).

In both seasons, it is evident that microclimate variables measured at sites with four, 17 and 31 years of succession are different as those measured in conserved areas. It is possible that these fragments may require longer periods to acquire abiotic conditions that resemble those found prior to disturbance. However, the intermediate succession categories (17 and 31 years succession), like categories four and 17 years of succession, exhibited similar microclimatic conditions during the wet season; this decrease in climate heterogeneity suggests that vegetation at the study area may experience a convergent successional trajectory (Walker, Wardle, Bardgett, & Clarkson, 2010), and microclimatic factors could be restored over time (Baker et al., 2014). In this way, it is possible that vegetation also changes with succession time till reaching the most conserved areas condition. This is of relevance for conservation, since distribution of native low thorn forest in the region has been reduced dramatically in the last years, and the existent fragments are surrounded by disturbed areas or sites with different succession time (Sánchez-Reyes et al., 2017). Therefore, it is necessary to assess whether this trend is maintained in plants as well as in other biological groups within the study area, or on the contrary, if current disturbed areas with early succession time may not recover over time to its original condition.

In summary, we found microclimate differences between successional categories, these results agree with similar findings in other works (Hojdová et al., 2005; Hardwick et al., 2015). However, microclimatic influence was higher in the dry than in the wet season, in contrast to other vegetal communities (Lebrija-Trejos et al., 2011). Although we presented evidence for such findings, it is possible that the sampling design may have influenced the results obtained, and therefore a higher number of replicates may be required for a better microclimatic characterization. Thus, further studies would be necessary in other areas of this endangered ecosystem to corroborate our conclusions. Regardless of the observed patterns, we document the importance of assessing microclimate changes during succession, since this is a key factor on species distribution (Swanson et al., 2011; Arroyo-Rodríguez et al., 2017). On the other hand, previous evidence suggests that successional trajectories of communities have very different ending points according to several factors (Bhaskar, Dawson, & Balvanera, 2014; Longworth et al., 2014; Letcher et al., 2015); contrarily, successional microclimatic changes can be relatively well

predicted for various ecosystems. For example, early successional areas are characterized by higher temperature and lower humidity (Hojdová et al., 2005; Hardwick et al., 2015; Letcher et al., 2015), while conserved stages are related to opposing microclimates (Chu et al., 2007; Lebrija-Trejos, Pérez-García, Meave, Bongers, & Poorter, 2010; Campetella et al., 2011). In the study area, the low thorn forest patterns found are similar to those reported in other works (Hardwick et al., 2015; Lienard et al., 2015), but arose because of other variables of higher importance. Indeed, such patterns may originate due to vegetation characteristics, which we point out as a main driver of the observed differences. Besides, the fact that microclimate significant differences were greater during the dry season is of major relevance, since other dry forests shown contrary outcomes (Lebrija-Trejos et al., 2011). It demonstrates that influence of seasonality is distinct according to vegetal communities evaluated. As a consequence, our results suggest that assessment and restoration strategies of low thorn forest in Northern Mexico must be designed particularly for this ecosystem. In this regard, other studies have noted that conservation strategies cannot be the same for all areas, and therefore, each particular ecosystem and its full spectrum of characteristics associated with succession must be taken into account (Christensen, 2014). This work may represent one of the first assessments and characterization of microclimate in low thorn forest in Mexico, demonstrating that observed successional patterns are particular for this ecosystem, and as such provide new information for conservation strategies of this endangered vegetal community.

Ethical statement: authors declare that they all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. A signed document has been filed in the journal archives.

ACKNOWLEDGMENTS

We would like thank Fatima Magdalena Sandoval Becerra, Ricardo Vizcaya, and José Norberto Lucio García for their valuable help during fieldwork. Financial support for this study was granted by the Consejo Nacional de Ciencia y Tecnología (CONACYT) (Doctoral scholarship No. 401277). Also, we acknowledge facilities provided by the Tecnológico Nacional de México-Instituto Tecnológico de Cd. Victoria to accomplish this work.

RESUMEN

Variación microclimática estacional en un gradiente sucesional de selva baja espinosa en el Noreste de México. El aumento global en el cambio de cobertura vegetal y la deforestación han fragmentado una elevada proporción de áreas de vegetación nativa. El microclima es un factor que se modifica después de la pérdida de vegetación, y los efectos de tales perturbaciones son trascendentales para las especies. Sin embargo, tanto la sucesión secundaria como la estacionalidad implican modificaciones adicionales en el medio abiótico después del disturbio. Aunque los patrones microclimáticos durante la sucesión son conocidos en varios ecosistemas, no se han evaluado en áreas de selva baja espinosa, que constituye un ecosistema amenazado en el norte de México. La medición de tales factores microclimáticos es crucial para comprender las consecuencias de la recuperación post-disturbio en las especies. Por lo tanto, el objetivo del estudio fue evaluar la variación estacional del microclima en un gradiente de sucesión de cuatro categorías (áreas conservadas, 31, 17 y cuatro años de sucesión), delimitadas mediante imágenes de satélite LANDSAT (1973, 1986, 2000, 2005 y 2013) en un fragmento de selva baja espinosa en el noreste de México. Para caracterizar el microclima se consideraron la velocidad del viento, temperatura, humedad relativa, índice de calor, punto de rocío y evapotranspiración. Las variables se midieron de forma mensual, durante un año, en ocho sitios de muestreo en cada una de las cuatro categorías sucesionales, durante dos estaciones diferentes: húmeda (mayo a octubre 2016) y seca (noviembre 2016 hasta abril 2017). A través de un análisis multivariado de funciones discriminantes, se determinó que las categorías sucesionales en la selva baja espinosa son diferentes dependiendo del microclima. En la estación húmeda, las áreas con poco tiempo de sucesión se caracterizaron por valores más altos de índice de calor y velocidad del viento, al contrario de las áreas conservadas. En la estación seca, las diferencias sucesionales se atribuyeron a la velocidad del viento y la humedad relativa. Además, tanto la discriminación entre categorías como la importancia de las variables fueron mayores solo durante la estación seca. Por lo tanto, la



estacionalidad determina los patrones microclimáticos durante la sucesión secundaria. Además, cada categoría sucesional representa condiciones microclimáticas únicas, pero difieren de las áreas conservadas incluso después de 31 años de sucesión. De acuerdo con nuestros resultados, la estacionalidad y el microclima son de gran relevancia para el estudio de la sucesión secundaria. Se sugiere considerar ambos factores cuando se implementan programas de conservación de ecosistemas en riesgo, como la selva baja espinosa en el noreste de México. Al ser este un ecosistema poco estudiado, la caracterización microclimática que aquí se proporciona, ayudará a un mejor entendimiento y manejo forestal de dichas áreas.

Palabras clave: perturbación; sucesión secundaria; ambiente abiótico; estacionalidad; sistemas de información geográfica.

REFERENCES

- Aide, T. M., Clark, M. L., Grau, H. R., López-Carr, D., Levy, M. A., Redo, D., ... Muñiz, M. (2012). Deforestation and reforestation of Latin America and the Caribbean (2001-2010). *Biotropica*, 45(2), 262-271.
- Almaguer-Sierra, P. (2005). Fisiografia del Estado de Tamaulipas. In L. Barrientos-Lozano, A. Correa-Sandoval, J. V. Horta-Vega, & J. García-Jiménez (Eds.), *Biodiversidad Tamaulipeca* (Vol. 1, pp. 2-20). Victoria, Tamaulipas, México: Dirección General de Educación Superior Tecnológica, Instituto Tecnológico de Cd. Victoria.
- Anderson, G. B., Bell, M. L., & Peng, R. D. (2013). Methods to calculate the heat index as an exposure metric in environmental health research. *Environmental Health Perspectives*, 121(10), 1111-1119.
- Arroyo-Rodríguez, V., Melo, F. P. L., Martínez-Ramos, M., Bongers, F., Chazdon, R. L., Meave, J. A., ... Tabarelli, M. (2017). Multiple successional pathways in human-modified tropical landscapes: new insights from forest succession, forest fragmentation and landscape ecology research. *Biological Reviews*, 92(1), 326-340.
- Baker, T. P., Jordan, G. J., Steel, E. A., Fountain-Jones, N. M., Wardlaw, T. J., & Baker, S. C. (2014). Microclimate through space and time: microclimatic variation at the edge of regeneration forests over daily, yearly and decadal time scales. *Forest Ecology and Management*, 334, 174-184.
- Bhaskar, R., Dawson, T. E., & Balvanera, P. (2014). Community assembly and functional diversity along succession post-management. *Functional Ecology*, 28(5), 1256-1265.
- Bernhardt-Römermann, M., Gray, A., Vanbergen, A. J., Bergès, L., Bohner, A., Brooke, R. W., ... Stadler, J. (2011). Functional traits and local environment

predict vegetation responses to disturbance: a pan-European multi-site experiment. *Journal of Ecology*, *99*(3), 777-787.

- Breugel, M., Martínez-Ramos, M., & Bongers, F. (2006). Community dynamics during early secondary succession in Mexican tropical rain forests. *Journal of Tropical Ecology*, 22(6), 663-674.
- Campetella, G., Botta-Dukát, Z., Wellstein, C., Canullo, R., Gatto, S., Chelli, S., ... Bartha, S. (2011). Patterns of plant trait–environment relationships along a forest succession chronosequence. *Agriculture, Ecosystems* & *Environment, 145*(1), 38-48.
- Ceballos, G., Martínez, L., García, A., Espinoza, E., Creel, J. B., & Dirzo, R. (2010). *Diversidad, amenazas y* áreas prioritarias para la conservación de las selvas secas del Pacífico de México. D.F., México: Fondo de Cultura Económica, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.
- Challenger, A., & Soberón, J. (2008). Los ecosistemas terrestres. In CONABIO (Ed.), *Capital natural de México, Conocimiento actual de la biodiversidad* (Vol. I, pp. 87-108). D.F., México: Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.
- Checa, M. F., Rodríguez, J., Willmott, K. R., & Liger, B. (2014). Microclimate variability significantly affects the composition, abundance and phenology of butterfly communities in a highly threatened Neotropical dry forest. *Florida Entomologist*, 97(1), 1-13.
- Chu, C. J., Wang, Y. S., Du, G. Z., Maestre, F. T., Luo, Y. J., & Wang, G. (2007). On the balance between niche and neutral processes as drivers of community structure along a successional gradient: Insights from alpine and sub-alpine meadow communities. *Annals* of Botany, 100(4), 807-812.
- Christensen, N. L. (2014). An historical perspective on forest succession and its relevance to ecosystem restoration and conservation practice in North America. *Forest Ecology and Management*, 330, 312-322.
- Craven, D., Hall, J. S., Berlyn, G. P., Ashton, M. S., & Breugel, M. v. (2015). Changing gears during succession: shifting functional strategies in young tropical secondary forests. *Oecologia*, 179(1), 293-305.
- Damschen, E. I., Baker, D. V., Bohrer, G., Nathan, R., Orrock, J. L., Turner, J. R., ... Tewksbury, J. J. (2014). How fragmentation and corridors affect wind dynamics and seed dispersal in open habitats. *Proceedings of the National Academy of Sciences*, 111(9), 3484-3489.
- Davies-Colley, R. J., Payne, G. W., & Elswijk, M. (2000). Microclimate gradients across a forest edge. New Zealand Journal of Ecology, 24(2), 111-121.

- Esri (2013). ArcGIS 10.2 for Desktop 1999-2013. Redlands, CA, USA: Environmental Systems Research Institute Inc.
- Ewers, R. M., & Banks-Leite, C. (2013). Fragmentation impairs the microclimate buffering effect of tropical forests. *PLoS ONE*, 8(3), e58093.
- Ferraz, S. F. B., Ferraz, K. M. P. M. B., Cassiano, C. C., Brancalion, P. H. S., da Luz, D. T. A., Azevedo, T. N., ... Metzger, J. P. (2014). How good are tropical forest patches for ecosystem services provisioning? *Landscape Ecology*, 29(2), 187-200.
- Foley, J. A., DeFries, R., Asner, G. P., Barford, C., Bonan, G., Carpenter, S. R., ... Snyder, P. K. (2005). Global consequences of land use. *Science*, 309(5734), 570-574.
- Frey, S. J. K., Hadley, A. S., Johnson, S. L., Schulze, M., Jones, J. A., & Betts, M. G. (2016). Spatial models reveal the microclimatic buffering capacity of oldgrowth forests. *Science Advances*, 2(4), e1501392.
- García-Morales, L. J., Estrada-Castillón, A. E., García-Jiménez, J., Villarreal-Quintanilla, J. A., Cantú-Ayala, C., ... Vargas-Vázquez, V. A. (2014). Florística y vegetación del Área Natural Protegida Altas Cumbres, Tamaulipas, México. In A. Correa-Sandoval, J. V. Horta-Vega, J. García-Jiménez, & L. Barrientos-Lozano (Eds.), *Biodiversidad tamaulipeca* (Volumen 2, Número 1, pp. 15-73). Tamaulipas, México: Tecnológico Nacional de México, Instituto Tecnológico de Ciudad Victoria.
- Gehlhausen, S. M., Schwartz, M. W., & Augspurger, C. K. (2000). Vegetation and microclimatic edge effects in two mixed-mesophytic forest fragments. *Plant Ecology*, 147, 21-35.
- Global Land Cover Facility Global Land Survey (GLCF-GLS). (2016). Global Land Cover Facility (GLCF), Global Land Survey (GLS). Maryland, US. http:// www.landcover.org/data/gls/
- Global Visualization Viewer (GLOVIS). (2016). USGS Global Visualization Viewer (GLOVIS). United States Geological Survey Earth Resources Observation Systems. Retrieved from http://glovis.usgs.gov/
- Grimmond, C. S. B., Robeson, S. M., & Schoof, J. T. (2000). Spatial variability of micro-climatic conditions within a mid-latitude deciduous forest. *Climate Research*, 15, 137-149.
- Guariguata, M. R., & Ostertag, R. (2001). Neotropical secondary forest succession: changes in structural and functional characteristics. *Forest Ecology and Management*, 148(1-3), 185-206.
- Hansen, M. C., Potapov, P. V., Moore, R., Hancher, M., Turubanova, S. A., Tyukavina, A., ... Townshend, J. R. G. (2013). High-resolution global maps of

21st-century forest cover change. *Science*, *342*(6160), 850-853.

- Hardwick, S. R., Toumi, R., Pfeifer, M., Turner, E. C., Nilus, R., & Ewers, R. M. (2015). The relationship between leaf area index and microclimate in tropical forest and oil palm plantation: forest disturbance drives changes in microclimate. *Agricultural and Forest Meteorology*, 201, 187-195.
- Hojdová, M., Hais, M., & Pokorný, J. (2005). Microclimate of a peat bog and of the forest in different states of damage in the Šumava National Park. *Silva Gabreta*, 11(1), 13-24.
- Instituto Nacional de Estadística y Geografía (INEGI). (2013). Conjunto de datos vectoriales de uso del suelo y vegetación escala 1:250,000, Serie V (Capa Unión). Aguascalientes, México: Instituto Nacional de Estadística y Geografía.
- James, F. C., & McCulloch, C. E. (1990). Multivariate analysis in ecology and systematics: panacea or Pandora's Box? *Annual Review of Ecology, Evolution, and Systematics, 21*(1), 129-166.
- Karels, T. J., Bryant, A. A., & Hik, D. S. (2004). Comparison of discriminant function and classification tree analyses for age classification of marmots. *Oikos*, 105(3), 575-587.
- Kovács, B., Tinya, F., & Ódor, P. (2017). Stand structural drivers of microclimate in mature temperate mixed forests. Agricultural and Forest Meteorology, 234, 11-21.
- Lebrija-Trejos, E., Pérez-García, E. A., Meave, J. A., Bongers, F., & Poorter, L. (2010). Functional traits and environmental filtering drive community assembly in a species-rich tropical system. *Ecology*, 91, 386-398.
- Lebrija-Trejos, E., Pérez-García, E. A., Meave, J. A., Poorter, L., & Bongers, F. (2011). Environmental changes during secondary succession in a tropical dry forest in Mexico. *Journal of Tropical Ecology*, 27(5), 477-489.
- Lee, D., & Brenner, T. (2015). Perceived temperature in the course of climate change: an analysis of global heat index from 1979 to 2013. *Earth System Science Data*, 7(2), 317-344.
- Letcher, S. G., Lasky, J. R., Chazdon, R. L., Norden, N., Wright, S. J., Meave, J. A., ... Williamson, G. B. (2015). Environmental gradients and the evolution of successional habitat specialization: a test case with 14 Neotropical forest sites. *Journal of Ecology*, 103(5), 1276-1290.
- Lienard, J., Florescu, I., & Strigul, N. (2015). An appraisal of the classic forest succession paradigm with the shade tolerance index. *PLoS ONE*, 10(2), e0117138.
- Lohbeck, M., Poorter, L., Martínez-Ramos, M., Rodríguez-Velázquez, J., Breugel, M. V., & Bongers, F. (2014).

Changing drivers of species dominance during tropical forest succession. *Functional Ecology*, 28(4), 1052-1058.

- Longworth, J. B., Mesquita, R. C., Bentos, T. V., Moreira, M. P., Massoca, P. E., & Williamson, G. B. (2014). Shifts in dominance and species assemblages over two decades in alternative successions in Central Amazonia. *Biotropica*, 46(5), 529-537.
- Melo, F. P. L., Arroyo-Rodríguez, V., Fahrig, L., Martínez-Ramos, M., & Tabarelli, M. (2013). On the hope for biodiversity-friendly tropical landscapes. *Trends in Ecology & Evolution*, 28(8), 462-468.
- Miranda, F., & Hernández, E. (1963). Los tipos de vegetación en México y su clasificación. Boletín de la Sociedad Botánica de México, 28, 29-179.
- Norris, C., Hobson, P., & Ibisch, P. L. (2012). Microclimate and vegetation function as indicators of forest thermodynamic efficiency. *Journal of Applied Ecology*, 49(3), 562-570.
- Parr, C. L. (2012). Unpacking the impoverished nature of secondary forests. *Journal of Animal Ecology*, 81(5), 937-939.
- Pickett, S. T. A., Cadenasso, M. L., & Meiners, S. J. (2008). Ever since Clements: from succession to vegetation dynamics and understanding to intervention. *Applied Vegetation Science*, 12(1), 9-21.
- Pozo-Díaz, M. Z., & Carrasco, G. I. (2005). Aplicación del análisis discriminante a un conjunto de datos vinícolas mediante el paquete estadístico SPSS v10. *Tecnociencia*, 7(1), 7-21.
- Pulsford, S. A., Lindenmayer, D. B., & Driscoll, D. A. (2016). A succession of theories: purging redundancy from disturbance theory. *Biological Reviews*, 91(1), 148-167.
- Renaud, V., Innes, J. L., Dobbertin, M., & Rebetez, M. (2010). Comparison between open-site and belowcanopy climatic conditions in Switzerland for different types of forests over 10 years (1998–2007). *Theoretical and Applied Climatology*, 105(1-2), 119-127.
- Rencher, A. C. (2002). *Methods of multivariate analysis, second edition*. New York, USA: John Wiley & Sons, Inc.
- Sánchez-Reyes, U. J., Niño-Maldonado, S., Barrientos-Lozano, L., Jones, R. W., & Sandoval-Becerra, F. M. (2015). Análisis del nicho ecológico de Cryptocephalinae (Coleoptera: Chrysomelidae) en la Sierra de San Carlos, Tamaulipas, México. *Entomología Mexicana*, 2, 526-532.

- Sánchez-Reyes, U. J., Niño-Maldonado, S., Barrientos-Lozano, L., & Treviño-Carreón, J. (2017). Assessment of land use-cover changes and successional stages of vegetation in the Natural Protected Area Altas Cumbres, Northeastern Mexico, using Landsat satellite imagery. *Remote Sensing*, 9(712), 1-33.
- Sandoval-Becerra, F. M., Niño-Maldonado, S., Sánchez-Reyes, U. J., Horta-Vega, J. V., Venegas-Barrera, C. S., & Martínez-Sánchez, I. (2017). Respuesta de la comunidad de Chrysomelidae (Coleoptera) a la variación microclimática en un fragmento de bosque de encino del noreste de México. *Entomología Mexicana*, 4, 514-518.
- Schurr, F. M., Bond, W. J., Midgley, G. F., & Higgins, S. I. (2005). A mechanistic model for secondary seed dispersal by wind and its experimental validation. *Journal of Ecology*, 93(5), 1017-1028.
- Secretaría de Gobierno. (2015). Decreto Gubernamental mediante el cual se aprueba el Programa de Manejo del Área Natural Protegida "Altas Cumbres", localizada en los municipios de Jaumave y Victoria, Tamaulipas. Ciudad Victoria, Tamaulipas, México: Órgano del Gobierno Constitucional del Estado Libre y Soberano de Tamaulipas, Periódico Oficial del Estado de Tamaulipas, Tomo CXL, Secretaría General de Gobierno.
- StatSoft Inc. (2007). STATISTICA (Data Analysis Software System), version 8.0. Retrieved from http:// www.statsoft.com
- Swanson, M. E., Franklin, J. F., Beschta, R. L., Crisafulli, C. M., DellaSala, D. A., Hutto, R. L., ... Swanson, F. J. (2011). The forgotten stage of forest succession: early-successional ecosystems on forest sites. *Frontiers in Ecology and the Environment*, 9(2), 117-125.
- Trejo, I. (2010). Las selvas secas del Pacífico mexicano. In G. Ceballos, L. Martínez, A. García, E. Espinoza, J. B. Creel, & R. Dirzo (Eds.), Diversidad, amenazas y áreas prioritarias para la conservación de las selvas secas del Pacífico de México (pp. 41-51). D.F., México: Fondo de Cultura Económica, Comisión Nacional para el Conocimiento y Uso de la Biodiversidad.
- Treviño-Carreón, J., & Valiente-Banuet, A. (2005). La vegetación de Tamaulipas y sus principales asociaciones vegetales. In L. Barrientos-Lozano, A. Correa-Sandoval, J. V. Horta-Vega, & J. García-Jiménez (Eds.), *Biodiversidad tamaulipeca Vol. 1* (pp. 22-46). Ciudad Victoria, Tamaulipas, México: Dirección General de Educación Superior Tecnológica, Instituto Tecnológico de Ciudad Victoria.
- Walker, L. R., Wardle, D. A., Bardgett, R. D., & Clarkson, B. D. (2010). The use of chronosequences in studies of ecological succession and soil development. *Jour*nal of Ecology, 98(4), 725-736.