Stand structure and woody species composition along a fire chronosequence in mixed pine-oak forest, Mexico.

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Abstract
Although forest fires have become a critical question in Mexico following the fire season of 1998, there is little knowledge regarding the effects of fire events on forest structure, composition, and dynamics in mixed pine-oak forests in northern Mexico. Objective of this study was to determine how fire has shaped forest structure and composition in mixed pine-oak forests and to describe trends and stages of natural succession. First of all, a chronosequence of forest fires was reconstructed by carrying out tree ring analysis and inventories in different sites of increasing time since fire. Increments cores were taken from \emph{P. teocote} and \emph{P. pseudostrobus}. Stand level vegetation characteristics, environmental data (solar radiation, slope, aspect, and elevation) were analysed along a 134 year chronosequence at 23 sites in mixed forests of the Ecological Park "Chipinque" in the Sierra Madre Oriental. Detrended canonical analysis confirmed that the time since fire was correlated to most biotic variables and indicates that the disturbance regime is tightly coupled to ecosystem functions. The study revealed that there were important differences between post-fire cohorts in terms of species richness, stand composition, and structure. High tree diversity was generally found in young stands, while the intermediate and major ones showed the lowest woody plant diversity. In old stands, tree diversity was increased again. In turn, the forest structure was less divers in young stands compared to intermediate, major and old stands. By exploring forest stand structure and composition in the context of ecosystem functions an overlook of fire ecology in northern Mexican pine-oak forests was gained. The occurrence of forest fires is natural part of these mixed forests and sustainable forest management should include the natural forest fire incidence to maintain forest health and the possibility to benefit from this natural resource.

Introduction
Fire disturbance is a major factor driving patterns of vegetation structure and composition in natural ecosystem (Whelan, 1995). Human activities can influence natural fire regimes by increasing fires in forests that would seldom burn under natural conditions (Goldammer, 2003). To determine the extent of human influence on natural fire regimes, many research projects have focused on fire effects and forest structure in many countries, especially in the USA, Canada, and Australia. These countries have developed strategies to manage forest fires, but have also learned to accept fires as a natural disturbance that must be integrated into restoration programs,
conservation, and management (Wouters, 1994; Bergeon et al., 2003; Russell et al., 2004; Stephens and Ruth 2005).

According to Rodriguez-Trejo and Fulé (2003), forest fires are widespread throughout Mexican forest ecosystems. In 1998, around 9,000 fires burned approximately 220,000 ha of forest land. In 2003, around 100,000 ha of forested area were lost, and as of April 2006, approximately 80,000 ha have burned (CONAFOR, 2006).

Rodriguez-Trejo and Fulé (2003) identified several types of fire-dependent (or adapted) traits (e.g. serotiny, seed germination post-fire sprouting and fast initial growth) that are evident in a majority of Mexican pine species. Besides providing an increased understanding of species-specific fire traits in these forest types, it would also be important to investigate post-fire succession and the present forest structure in order to develop sustainable forest management strategies for Mexican pine-oak forests where human interference has been minimal. These areas can provide a reference baseline for managers to strive for where restoration may be necessary.

Owing to the current state of knowledge and the increasing demand for detailed information about forest fires in northern Mexico, this study will provide data on natural succession and changes in woody plant composition after fire events. Our study objectives were to quantify present forest structure and woody plant species composition along a fire chronosequence in pine-oak forest in the SMO to (1) assist in the development of restoration objectives for similar forest in northeast Mexico and, (2) to assess the species-specific fire traits and forest succession patterns within the SMO, and (3) increase our understanding of mixed pine-oak forest in the SMO.

Materials and Methods

Research area

The investigation was carried out in the Ecological Park “Chipinque” (PECH), which is part of the National Park “Cumbres de Monterrey” in the northern part of the “Sierra Madre Oriental” in Northeast Mexico. The PECH is located in the State Nuevo Leon near the state's capital “Monterrey” and extends over a territorial area of 1,624 ha (25°34´ to 25°38´ N and 100°18´ to 100°24´ W) between 650 m and 1,800 m above sea level (Alanís et al., 1995). The climate is determined by two seasons: hot summers from May to October and cold winters from November to April. The mean annual temperature is 22.3°C (1977 to 2001) and the mean annual total precipitation is 602 mm (1958 to 2001). Around 78% of the rainfall occurs during the hot months. February is the driest month with a mean monthly total of 16.3 mm of precipitation (CNA, 2004). The most common soil type in the PECH is lithosol (PNCM 2003). Three main vegetation types are distinguished in the Sierra Madre Oriental: the “matorral submontano” in the lower parts, the oak forests in the middle altitudes and the pine-oak forests in the higher parts of the mountain range.

Selection of study sites and vegetation measurements

For this study we selected sites belonging to the vegetation type pine-oak forest, located in the higher parts of the Sierra Madre Oriental. Stands (= post-fire cohorts) were chosen by stratifying the study area by aspect and stand fire history. The post-fire stands were selected according to the chronosequence (space for time substitution) approach (Yanai et al., 2003).

The extension of the burn area of each post-fire cohort was reconstructed using visual delineators including bole scars and charcoal remains in the surface soil. A comprehensive fire history was developed using tree ring analysis. Increment cores were taken from P. teocote and P. pseudostrobus. After sanding and polishing fires scares were distinguished with a microscope.
The year of each fire was identified by cross-dating tree rings. Based on this survey we identified five post fire cohorts on the north aspect and four post-fire cohorts on the south aspect (Table 1). Depending on the size of the burned area, one to four circular plots (1000 m$^2$) were established within each stand. The centers of the plots were located using a 300 x 300 m grid system (González Tagle et al. 2005). In total we measured 23 plots. In each plot tree density, tree height and tree diameter were recorded for all woody plant species with a diameter at breast height (DBH 1.3 m above ground level) $\geq$ 5 cm (in post-fire cohort PECH98 all woody stems over 1.3 m height). The coefficient of variation (CV) of the tree diameter was calculated as an indicator of the structural complexity of each post-fire cohort (Fowler et al. 2004).

Table 1.- Environmental characteristics of the stands in the PECH.

<table>
<thead>
<tr>
<th>Stands</th>
<th># of plots</th>
<th>Fire year</th>
<th>tsf*</th>
<th>aspect</th>
<th>slope (°)</th>
<th>elevation (m)</th>
<th>gromeadow**</th>
</tr>
</thead>
<tbody>
<tr>
<td>PECH98</td>
<td>3</td>
<td>1998</td>
<td>4</td>
<td>NE</td>
<td>23</td>
<td>1125</td>
<td>72.3 ± 11.0</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>1998</td>
<td>4</td>
<td>SE</td>
<td>36</td>
<td>1220</td>
<td>79.2 ± 1.7</td>
</tr>
<tr>
<td>PECH84</td>
<td>3</td>
<td>1984</td>
<td>18</td>
<td>N</td>
<td>36</td>
<td>1300</td>
<td>77.3 ± 1.2</td>
</tr>
<tr>
<td></td>
<td>2</td>
<td>1984</td>
<td>18</td>
<td>S</td>
<td>30</td>
<td>1332</td>
<td>73.5 ± 5.9</td>
</tr>
<tr>
<td>PECH72</td>
<td>2</td>
<td>1972</td>
<td>30</td>
<td>N</td>
<td>23</td>
<td>1380</td>
<td>76.1 ± 0.1</td>
</tr>
<tr>
<td></td>
<td>4</td>
<td>1972</td>
<td>30</td>
<td>S</td>
<td>22</td>
<td>1370</td>
<td>73.9 ± 2.7</td>
</tr>
<tr>
<td>PECH40</td>
<td>3</td>
<td>1940</td>
<td>62</td>
<td>NE</td>
<td>27</td>
<td>1300</td>
<td>78.0 ± 3.9</td>
</tr>
<tr>
<td></td>
<td>1</td>
<td>1940</td>
<td>62</td>
<td>S</td>
<td>26</td>
<td>1206</td>
<td>80.2</td>
</tr>
<tr>
<td>PECH868</td>
<td>3</td>
<td>1868</td>
<td>134</td>
<td>N</td>
<td>28</td>
<td>1195</td>
<td>82.0 ± 0.1</td>
</tr>
</tbody>
</table>

*tsf= time since fire, ** gromeadow = mean solar radiation during growing season (May-December)

The importance value index (IVI) of each woody plant species was calculated using the relative density (RD), relative dominance (RDom), and relative frequency (RF) (Coroi et al., 2004). Species richness (S) represents the total number of woody plant species in each post-fire cohort. We applied the Shannon evenness measure as an index of comparative diversity ($J'$, Magurran 2004). In order to examine the changes in woody plant species diversity between post-fire cohorts along the chronosequence, the Whittaker’s measure $\beta_W$ was calculated (Magurran, 2004).

**Environmental parameters**

Environmental parameters (aspect, slope, elevation, time since fire, and potential solar radiation) were obtained and their influences on woody plant species richness were examined. Slope, aspect and elevation were taken from a digital elevation model (DEM) based on a 1:50000 map of the area (INEGI, 2003). Potential solar radiation (PSR) was estimated for each plot and each hour of the growing season (May-December) using a Geographical Information System (GIS) (Müller-Using, 1994, Gallegos et al., 1997; Schulz, 2003). The input data were elevation, solar inclination angle, solar azimuth, and shadow effects (Gallegos et al., 1997; Schulz, 2003). The environmental parameters of all post-fire cohorts in the PECH are summarized in Table 1.
Cluster and detrended correspondence analysis

Species abundance data from each sampling plot (survivor trees from former fires were excluded) were summarized as plot counts and log\([x+1]\) transformed to reduce the ranges of species variation (Jongman et al., 1995). Environmental variables (slope, aspect, elevation, time since fire, and growmeadow) were also summarized as plot averages and appropriately transformed. Because aspect is a circular variable, we transformed it into one derived variable “southness”, where \(\text{southness} = 180 - |\text{aspect} - 180|\) to provide an interpretable directional variable (Chang et al., 2004).

Graphical examination and correlation statistics were then used to assess the importance of environmental factors determining the major species DCA axes (Oksanen et al., 2002). DCA ordinations were conducted using the R statistical program which utilizes a community ecology package (Oksanen et al., 2002) and incorporate the function DECORANA which is a faithful port of Mark Hill’s program with the same name (Oksanen et al., 2002) with corrections for instability of rescaling functions following Oksanen and Minchin (1997).

Statistical analyses

Tree height and DBH distribution for all woody plant species was skewed by numerous outliers, and even the transformation of these data did not meet the assumptions of parametric statistics. Furthermore, due to the small sample size it was not possible to test for normality. Therefore, nonparametric tests were applied (Conover, 1999). Data for each aspect were rank transformed. The Kruskall-Wallis analysis followed by Dunn’s test for multiple comparisons of unbalanced data was used to test for differences in woody plant species richness and evenness between post-fire cohorts at \(P<0.05\) (Zar, 1999).

Results

Forest structure and woody plant species composition

Tree density on the north aspect was highest in PECH98 (3400 trees ha\(^{-1}\)) and lowest in PECH40 (753 trees ha\(^{-1}\)). On the south aspect, tree density ranged from 850 trees ha\(^{-1}\) in PECH40 to 1417 trees ha\(^{-1}\) in PECH72. On the north aspect mean DBH ranged from 3.1 cm (PECH98) to 22.7 cm (PECH40). A similar DBH range was found for the stands on the south aspect. Coefficient of variation of DBH on the north aspect was highest (0.69) in the mature post-fire cohort (PECH868), indicating a high structural complexity. In contrast, on the south aspect, the structural complexity (CV=0.63) was highest in the youngest post-fire cohort (PECH98). Mean tree height on the north aspect varied between 2.1 m (PECH98) to 13.1 m (PECH40). On the south aspect, mean tree heights ranged from 2.7 m (PECH98) to 8.9 m (PECH40). Average basal area on the north aspect ranged from 3.4 m\(^2\) ha\(^{-1}\) (PECH98) to 37.3 m\(^2\) ha\(^{-1}\) (PECH40). On the south aspect the mean basal area was 2.2 m\(^2\) ha\(^{-1}\) in PECH98 and 38.9 m\(^2\) ha\(^{-1}\) in PECH40.

The most important woody species across the chronosequence on the north aspect were Quercus rysophylla, as it had the highest importance value index, followed by Pinus teocote, Quercus canbyi and Pinus pseudostrobus. Quercus rysophylla was dominant in the youngest and intermediate post-fire cohorts, and co-dominant in the mature and old post-fire cohorts. Pinus teocote was dominant in the mature post-fire cohort, while Pinus pseudostrobus was dominant only in the oldest stands (PECH868). Quercus canbyi was co-dominant across the chronosequence. On the south aspect, Q. canbyi, Q. virginiana, and P. teocote were the most important woody plant species. Q. canbyi was dominant while Q. virginiana was co-dominant in the intermediate post-fire cohorts. In the mature stands, P. teocote was the dominant species whereas Pinus pseudostrobus was always present as co-dominant across the chronosequence. In the young post-fire cohorts, Arbutus xalapensis, Ceanothus coeruleus, and Cercis canadensis were found on both aspects.
Woody plant species richness and diversity

On the north aspect we found five different post-fire cohorts with 16 woody plant species and 3,132 individuals. Four post-fire cohorts were identified on the south aspect with 12 woody plant species and 1,202 individuals. On the north aspect significant differences in woody plant species richness were found across the chronosequence (P<0.021). PECH868 had the highest species richness (10.7 spp. 1000 m^-2). The mature post-fire cohort (PECH40) was poor in species (3.7 spp. 1000 m^-2). In contrast, we did not find significant differences in woody plant species richness among post-fire cohorts on the south aspect. Woody plant species richness ranged between 5 and 6 spp. 1000 m^-2. The Shannon evenness measure on the north aspect was inversely correlated with woody plant species richness, and the Kruskall-Wallis test showed significant differences (P<0.03) between the post-fire cohorts, while on the south aspect no significant differences were found. The post-fire cohorts on the north aspect showed higher temporal woody plant species turnover rates ($\beta_{\text{north}} = 2.5$) as compared to the south aspect ($\beta_{\text{south}} = 2.1$). On the north aspect, the mature stand had a higher woody plant species turnover rate ($\beta = 3.3$) than those of the intermediate and youngest stands. On the south aspect, the highest turnover rate was found in the young stand (PECH98, $\beta = 1.4$) and the lowest in the intermediate ($\beta = 1.0$) and mature stand ($\beta = 1.0$).

Cluster and detrended correspondence analysis

Hierarchical cluster analysis identified five groups with similar characteristics (Figure 1). Group 1 included all plots which established after the fire in 1984 and 1972 on the south aspect. Group 2 encompassed all plots (north and south aspect) of PECH40. All plots from PECH860 belonged to Group 3, sharing two species (Quercus rysophylla and Pinus teocote) with the highest IVI values (Table 3). Group 4 included all plots on the north aspect which established after the fire in 1984 and 1972. All plots from the youngest post-fire cohort (PECH98 north and south) were found in Group 5 (Figure 2).

![Hierarchical cluster analysis from the 23 plots in the PECH, Mexico](Figure 1)

The Detrended Canonical Analysis (including all 23 plots) revealed that most of the south aspect plots were well-separated from the plots of north aspect (Figure 3). This ordination also illustrated that most of the south aspect plot occurred close to each other. Results from DCA identified that the distribution of the plots along axis DCA 1 was influenced by the variable southness. The axis DCA 2 was interpreted as a time since fire gradient (Figure 2). The DCA eigenvalues of axes DCA1 and DCA2 were considerably higher than those of axes 3 and 4,
indicating that most of the extractable variance in species composition can be accounted by the first and second DCA axes. These axes explained 29% and 16% of the variance in the DCA. When DCA scores were compared to environmental variables, the first DCA axis was strongly correlated to variable southness (P>0.001), and related to growmeadow and slope, the second axis was highly correlated to variable time since fire (tsf, P>0.001).

Figura 2 DCA ordination diagram with log transformed data in the PECH. The scale refers to multiples of the standard deviation (sd), tsf = time-since-fire.

Discusión

Changes in Forest structure after fire
As a fact different succession stages have their own specific stand structure. Initially, the findings demonstrated significant differences in mean diameter, mean height, basal area, and stand volume between the stages. In early succession stages, a high establishment of saplings and sprouts occurring in forests stands after wildland fires events, have been documented by several authors (Fulé and Covington, 1994, 1996, 1997, 1999, Huang, 1997).

In general, the highest species richness was observed in young post-fire cohorts and above all on the north-facing slopes. Excluding the oldest post-fire (PECH-868), the species richness tended to decline in intermediate and major post-fire cohorts, as the biomass and cover of woody plants continued to increase. Jiménez and Aguirre (1999) have found 34 plant species in the PECH one year after the forest fire disturbance in 1998.

The decline of species richness in time after forest fire disturbance might be caused primarily by the elimination of some early species, which were overtopped and shaded out by rapidly growing woody plants, especially resprouters (Miller, 2000). The effect of declining species richness was also documented by Gill et al. (1999) as a characteristic in arid and semi-arid forested regions, such as the studied mixed pine-oak forest in the PECH. Furthermore, species, invading after fire occurrence, must be able to tolerate a wide range of established circumstances or rather require some condition present in established communities (Gill et al., 1999). In general, the north-facing slopes were covered by more trees and shrub species leading to a higher stand complexity, than the south-facing slopes in the PECH. This was also consistent with observations done on the chaparral vegetation on north-facing slopes in California, where north-facing slopes showed also a higher plant species richness and plant abundance than the south-facing ones (Guo, 2001). Compared with south-facing slopes, higher species turnover rates on north-facing slopes within the research area may be explained with the larger species pool of 17 species compared with only 13 on south-facing slopes. Concerning species richness, a high number of species results with in higher community stability or rather resilience (Guo, 2001). In mountainous terrain, vegetation is
often closely associated with topography (Chang, 2004). In this study, using the gradient analysis method (DCA) the topographic position (variables slope and southness) was found to be the most important factor determining species composition in the PECH. Similar studies have shown that the importance of the topographic position may be further associated with the moisture gradient or wind exposure, that are highly influenced by topography (Chang, 2004).

**Conclusion**

The historical documentation of wildland fire events in the PECH showed that five forest fires have occurred in 134 years. A shift in the regime has been observed. At first, the fire regime was characterized by widespread surface fires of probably low intensity, with a fire interval from four to six years. Later on, the fire regime changed and was characterized by less frequent, but more severe forest fires. Hence fire intervals of 14 to 20 years were detected after 1940. This change seemed to be highly influenced by human activities.

Changes of forest structure and biodiversity were registered in different successional stages. A high species was generally found in young post-fire cohorts, while the intermediate and major stands showed the lowest diversity. In old stands, diversity was increased again. In turn, the forest structure was less diverse in young stands compared to intermediate, major, and old stands, where structural diversity was highest. Comparing north- and south slopes, stands facing the North were generally more diverse, in structure as well as in species.

Furthermore, landscape patches and thereupon the diversity on landscape-scale (β diversity) seemed to be influenced by forest fire occurrence or rather even depended on fire disturbance. So, fire dependent species were registered within the research area and fire occurrence has been natural part of ecological processes in pine-oak forests on northeast Mexico over many decades. Nevertheless, people still tend to combat and suppress forest fires, feeling endangered by wildland fires. Therefore, an exchange of information about fire ecology and fire management suggestions is required between fire ecologists and decision makers.

**References**


