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Climate change in forest ecosystems: A field experiment addressing the effects of raising temperature and reduced rainfall on early life cycle stages of oaks

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ABSTRACT

Higher temperatures and reduced rainfalls that are expected with the advance of climate change can impair the emergence and establishment of tree seedlings in forest ecosystems. These climatic changes can also decrease the availability of soil resources and reduce the performance of seedlings. We evaluated these effects in a temperate forest from Mexico with two native oak species (Quercus crassifolia and Quercus eduardii). As recently emerged oak seedlings are highly sensitive to changing environmental conditions, our field experiment was conducted across the season in which seedling emergence occurs (October-February). In the field, we used open-top chambers to increase temperature and rainout shelters to reduce rainfall, while controls were exposed to the current climate. Experimental plots of both treatments were established beneath the forest canopy because most oaks recruit in understory habitats. In these plots, we sowed acorns of both species in October 2015 and recorded seedling emergence and survival until February 2016, also monitoring temperature, precipitation and contents of water and nitrogen in the soil. On seedlings that survived until the end of the experiment we measured their growth, photosynthetic efficiency and foliar contents of water, carbon and nitrogen. Both the emergence and survival of Q. crassifolia seedlings were lower in climate change plots than in controls, but no differences were found for Q. eduardii. However, seedlings of both species had lower growth rates, photosynthetic efficiencies and contents of water, nitrogen and carbon in climate change simulation plots. These results indicate that climate change can impair tree seedling establishment in oak forest, also suggesting that their development will be constrained by reduced water and nitrogen availability.

1. Introduction

The prevalence of forest ecosystems mainly depends on the emergence and establishment of tree seedlings, but climate change can alter these processes (Clark et al., 2016). In temperate forests from North America, most global circulation models predict that the average air temperature will rise 5 °C in the course of this century, while annual precipitation levels in these ecosystems are projected to decrease up to 20% (IPCC, 2013). These ecosystems will then face warmer and drier conditions in the future, but field experiments assessing how tree seedlings will deal with these changes are still scarce.

Water availability is a key factor that regulates the emergence of

tree seedlings in forests and climate change can strongly impair this process (Pérez-Ramos et al., 2013; Clark et al., 2016). This is particularly critical for tree species that produce recalcitrant seeds because higher temperatures and lower precipitation levels can enhance seed water loss and induce embryo mortality, hence reducing seedling emergence (Zavala-Chávez, 2008; Joët et al., 2013). Further, if seed-lings emerge under these conditions, they can display a number of functional responses that would ultimately reduce their performance in climate change scenarios. Increased temperatures usually enhance fo-liar transpiration but, when plants are also subjected to water deficits, stomatal closure is induced to avoid excessive water loss and carbon fixation rates are reduced due to low gas exchange (Chaves et al., 2002;

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Haldimann and Feller, 2004; Rodriguez-Dominguez et al., 2016). Climate change can also affect light-dependent processes of photosynthesis in tree seedlings. This is because elevated thermal and/or water stress reduce the flow of electrons in the thylakoid membrane of chloroplasts and this decreases the conversion of light energy into chemical energy for fixing carbon (Maxwell and Johnson, 2000; Baker and Oxborough, 2004). Thus, the combined effects of warmer and drier conditions expected in forest ecosystems can alter water and carbon balances of tree seedlings and reduce their survival.

The availability of soil nitrogen is another important factor that can be altered by climate change. Nitrogen is the most important mineral nutrient that regulates plant growth (Poorter et al., 2012) and its natural inputs in forest ecosystems mainly depend on the activity of soil bacteria (Brookshire et al., 2011). These microorganisms are extremely sensitive to changes in soil temperature and moisture and, thus, the expected variations in climatic conditions can modify their efficiency for mineralizing nitrogen (Brookshire et al., 2011; Chen et al., 2011). However, the net effects of climate change on soil nitrogen are still controversial. This is because warming may stimulate the metabolic activity of nitrogen-fixing bacteria and increase soil nitrogen contents (Melillo et al., 2002; Brookshire et al., 2011; Butler et al., 2012), but reductions in soil moisture content due to reduced water inputs are expected to cause the opposite effects (Borken and Matzner, 2009; Chen et al., 2011). Instead, from the perspective of tree seedlings, the combined effects of increasing temperatures and reduced precipitation levels can jeopardize their ability to acquire nitrogen irrespective of whether its concentrations increase or decrease in the future. This is because these climatic conditions can induce strong water deficits and decrease the mobility of the mineral forms of nitrogen in the soil matrix, reducing the capability of plants to uptake this resource through the roots (Rennenberg et al., 2009; He and Dijkstra, 2014). In consequence, nitrogen contents and growth rates of tree seedlings in forest ecosystems are likely to decrease with the advance of climate change.

This study assesses how climate change could affect the emergence, survival and performance of recently emerged oak seedlings in a temperate forest of Mexico. For this, we performed a field experiment in which temperature and precipitation were manipulated during the period of the year in which the emergence of oak seedlings occurs, as these early life-cycle stages of oaks are extremely sensitive to changing environmental conditions (Zavala-Chávez and García-Moya, 1996; Badano et al., 2011, 2015). In these ecosystems, adult oaks produce acorns (nut-type, single-seeded fruits) in spring and release them in late summer, concurring with the second half of the rainy season (Zavala-Chávez and García-Moya, 1996; González-Salvatierra et al., 2013; Badano et al., 2015). As seeds of Mexican oaks are extremely recalcitrant (embryos die if seed water content drops below 25-30%) and they require elevated hydration levels to germinate (above 80% of seed water content), seedling emergence in the field occurs in short time after acorns are released from parental trees (Zavala-Chávez and García-Moya, 1996; Zavala-Chávez, 2008). The development of recently emerged oak seedlings mainly depends on the nutritional reserves accumulated in their cotyledons, but they are extremely susceptible to die because of thermal and water stress (Badano et al., 2009; González-Salvatierra et al., 2013). Thus, we hypothesized that warmer and drier conditions expected in climate change scenarios will reduce the emergence and survival of oak seedlings, also decreasing their overall performance. As climate change can reduce nitrogen availability for plants, we also hypothesized that the content of nitrogen in seedlings subjected to climate change conditions will be lower than those of seedling growing under the current climate.

2. Materials and methods

2.1. Study area

Our experiment was conducted at National Park "El Potosí", located

in the westernmost section of Sierra Madre Oriental (Sierra de Álvarez), state of San Luis Potosí, Mexico (include the file "Pérez Ruiz et al. Experimental sites.kmz" here). Climate in this region is temperate (mean annual temperature 18 °C) and up to 80% of rainfalls occurs between June and November (annual precipitation 500-600 mm), but sparse precipitation events can happen until January (Vargas-Márquez, 1997). Soils are shallow, with maximum depths of 10-15 cm, and vegetation is composed by semi-deciduous oak forests. In these ecosystems, despite the shallowness of soils, tree roots penetrate the bedrock through small fissures, anchoring these organisms to the substrate (Zavala-Chávez and García-Sánchez, 1999). As seedling emergence mainly occurs in the upper section of the soil profile of the forest understory (Badano et al., 2015), we located the experimental site beneath the canopy of a well-preserved oak forest dominated by Quercus crassifolia Humb. & Bonpl., Quercus eduardii Trel., and Quercus jonesii Trel. (21°55'10" N, 100°19'34" W, 2123 m elevation).

To determine how much climate will change in the study site, we computed the difference between current and future values of air temperature and precipitation using the geodatabases of Fernández-Eguiarte et al. (2012, 2014). These geodatabases provide the values of these two variables with a spatial resolution of 1-km² per pixel, where current values are monthly averages that integrate data from 1902 to 2011 (Fernández-Eguiarte et al., 2012) and future values are estimated for each month of the year with the HadGEM2-ES climate change model (Fernández-Eguiarte et al., 2014). Future values of air temperature and precipitation are provided for the period 2021-2040 and consider the four climate change scenarios (RCP2.6, RCP4.5, RCP6.0 and RCP8.5) proposed in the latest report of IPCC (2013). The HadGEM2-ES model is commonly used make climate change predictions across continental Mexico because it has lower deviations than other models when past climatic conditions are estimated, and this reduces uncertainty about the future climate (Fernández-Eguiarte et al., 2014). Because we focused on the earlier life-cycle stages of oaks, differences between current and future values of these climatic conditions were computed for the period of the year in which seedling emergence occurs, comprised between October and February. These estimates indicated that, during the tree recruitment season, air temperature in the study site will increase about 1.3-1.7 °C and precipitation will decrease by 11-18% (Table 1).

2.2. Experimental design

The field experiment was carried out between 17 October 2015 and 27 February 2016, comprising the entire period in which oak seedlings emerge and their early establishment occurs. For this, we draw a quadrant of 50×50 m in the study site and randomly selected 20 point-sites within it on September 2015, taking care of maintaining a minimum distance of 5 m among them. Leaf litter and rocks were removed in a radius of 3 m around each of these sites. The half of the sites were randomly assigned to climate change simulation plots (hereafter, CCS plots) where we manipulated temperature and precipitation, while the other half of the sites were assigned to control plots that were

Table 1

Short term changes (period 2021–2040) in air temperature and precipitation predicted for the study site during the oak recruitment season (October–February). Predictions were performed with the HadGEM2-ES model considering the four climate change scenarios (RCP2.6, RCP4.5, RCP6.0 and RCP8.5) proposed in the latest IPCC report.

Climate change scenario	Air temperature (net change)	Precipitation (percent change)
RCP2.6	+1.7 °C	-18%
RCP4.5	+1.2 °C	-14%
RCP6.0	+1.3 °C	-11%
RCP8.5	+1.3 °C	-16%

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