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PROGENY PERFORMANCE AND PATHOGEN ATTACK RELATIVE TO ELEVATION IN A NEOTROPICAL TREE

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HIGHLIGHTS

Kageneckia lanceolata is a vulnerable Neotropical tree distributed in mountain areas.

Seedling survival increased with elevation of the parent tree from 40 to 80%.

Damping-off was the only identified cause of seedling mortality under nursery conditions.

Seed mass, germination, and growth of seedlings were not influenced by elevation.

ABSTRACT

Climate and resource availability at the parent tree location are known to explain progeny characteristics; however, few studies have examined the role of resistance or tolerance to pathogens, even though climate is a main driver of pathogen abundance. We hypothesize that climate at the parent tree location has a relatively greater influence on progeny resistance or tolerance to pathogens than other progeny characteristics, such as seed mass or seedling growth. As a study species we used the vulnerable Neotropical tree *Kageneckia lanceolata* known to be susceptible to damping-off diseases. We collected seeds from 60 trees along the species entire elevational gradient in central Argentina as a surrogate for climatic gradient and selected an ample array of parent tree sizes and rockiness under the crown as surrogate of tree access to resources. Seedling survival in a common nursery significantly increased with elevation of the parent tree from 40 to 80 % ($P < 0.001$), with damping-off being the only identified cause of mortality. We also found a non-significant trend suggesting that proportional growth during the cold semester increased with elevation ($P = 0.083$). Seed mass, germination, and growth of seedlings were not significantly influenced by elevation ($P > 0.05$). Parent tree size and rockiness were not related to any of the measured progeny characteristics. We conclude that the pathogenic environment around parental plants might have a great influence on progeny resistance or tolerance to pathogens and suggest that incorporating the pathogen dimension into future progeny studies may yield important findings.

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INTRODUCTION

Progeny performance is influenced by a large array of ecological factors even under common garden conditions (i.e. Lira-Medeiros *et al.*, 2010). Sources of variation in performance include the climate at the parent tree location, nutrient resources captured by the parent tree and stored in the seed and accompanying tissues, and resistance or tolerance to pathogenic organisms (Fenner and Thompson, 2005; Vitasse *et al.*, 2013). In particular, pathogens greatly influence seedling performance thus being in some cases the main drivers of ecological processes such as tropical tree density-dependence seedling mortality (Spear *et al.*, 2015). However, in progeny studies, variation in resistance or tolerance to pathogenic organisms has rarely been the focus, even though understanding these issues could make tree breeding programs more efficient and help to predict the response of trees to changing conditions (Vivas *et al.*, 2015).

Variation in the resistance or tolerance to pathogens and to abiotic environmental conditions may be of genetic or phenotypic origin (Vivas *et al.*, 2015). Maternal effects, such as variation in nutrient resources stored in the seed and accompanying tissues, are mainly a response of the tree to resource availability. Tree size and rockiness under its crown may also be relevant factors influencing progeny performance. Large trees at sites with less proportion of rocks might have better access to nutrients due to a larger rhizosphere and may produce more and larger seeds that develop into more vigorous seedlings than smaller trees at sites with a higher proportion of rock (for the tree *Polylepis australis*, Renison *et al.*, 2004; Suarez *et al.*, 2008). Larger seed sizes might be correlated to higher seedling survival when attacked by pathogens (Vivas *et al.*, 2015).

Pathogens that cause damping-off to seedlings are relatively well widespread in the wild and especially easy to simulate in nursery conditions where damping off is an especially frequently reported disease; therefore, they may be an interesting group to focus progeny studies. Damping-off is caused by a group of soil-born fungus species that are known to affect seedlings in cool and damp soils (Tinus and McDonald, 1979; Muñoz-Castro *et al.*, 2015).

Here our objective was to explore the relative importance of climate and soil exploration capacity of parent trees on progeny resistance or tolerance to pathogens as compared to seed size, germination proportion and seedling growth. We hypothesize that climate and soil exploration capacity of parent trees have a relatively greater influence on progeny

resistance or tolerance to pathogens than other progeny characteristics. We expect an increase of seedling resistance or tolerance to damping-off with elevation of seed origin due to the decrease of soil temperature and increase in soil humidity, with relatively lower influence of elevation on other progeny metrics such as seed mass, germination proportion and growth of seedlings. We also expect an increase of seedling resistance or tolerance to damping-off with increasing soil exploration capacity of parent trees mediated by seed mass.

MATERIAL AND METHODS

Study area and species

The vegetation of the lower Córdoba Mountains in central Argentina corresponds to the Chaco Serrano district of the Gran Chaco Region. The climate is subtropical, with 85% of precipitation concentrated during the austral warm season from October to March. Mean annual precipitation averages 814 mm, with an increase of 21 mm for every 100 m in elevation, whereas mean annual temperature is 17.5 °C, with a decrease of 0.46°C per 100 m in elevation (Colladon *et al.*, 2014; Giorgis *et al.*, 2017). Our case study is a Neotropical tree that is known to undergo high seedling mortality due to damping-off (Eynard *et al.*, 2017). *Kageneckia lanceolata* Ruiz and Pav. (Rosaceae) (hereafter “*Kageneckia*”) is a small evergreen tree or shrub up to 7 m tall. The fruit is a pentamerous star-shaped capsule, about 2-3 cm in diameter; the seeds are winged and dispersed by wind (Demaio *et al.*, 2015). To the best of our knowledge, no specific studies have been conducted on its pollination biology, although its light yellowish flowers, radially symmetric, and with exposed reproductive organs suggest diurnal insect pollination (Fenster *et al.*, 2004). The distribution of this species includes a narrow strip along the dry Andean valleys and transition zones to the Puna of Peru, Bolivia and Argentina with a north-south extent of about 3200 km (latitudes of -7 to -33 degrees). The species has been categorized as vulnerable by IUCN (2017) with the main threats being grazing, habitat clearing and wood collection for fuel.

Seed collection and progeny trials

We collected seeds from six collection sites distributed along an elevational gradient, with the lowest and highest study trees being at 729 and 1286 m asl – representing a gradient of 557 m (Table 1), which was used as a surrogate for climate. Seed collection sites were separated by a minimum of 8 km and a maximum

of 60 km. For each parent tree we recorded: coordinates (degrees) and elevation (m asl) using a GPS (Garmin 24), parent tree height using a meter tape (cm) and proportion of the surface under the tree crown composed of rock (%; hereafter rockiness). Tree height was considered indicative of tree access to soil resources and rockiness was used as an inverse indicator of tree access to soil resources, i.e. the greater the percentage of rock surrounding trees the lower average soil exploration possibilities (see Suarez *et al.*, 2008 for *Polylepis australis*).

TABLE 1 Characteristics of the study sites and parental trees of the studied *Kageneckia lanceolata* seeds. Sites are arranged by elevation from 1 to 6, and in the columns we show the number of selected parental trees per site (N), elevation, geographic coordinates, rockiness and tree height. Values are averages per site \pm standard error and minimum and maximum values are indicated in parenthesis. Site names: 1. La Granja; 2. Cosquín; 3. Cuesta Blanca; 4. Vaquerías; 5. Km 65; 6. Cerro Blanco.

| Site | N | Elevation (m-asl) | Latitude Longitude | Rockiness (%) | Tree height (cm) |
|------|----|-------------------|--------------------|---------------|------------------|
| 1 | 11 | 763 \pm 10 | -31.039 | 15 \pm 6 | 399 \pm 19 |
| | | (729-838) | -64.280 | (1-55) | (250-500) |
| 2 | 9 | 814 \pm 25 | -31.243 | 14 \pm 7 | 416 \pm 49 |
| | | (711-892) | -64.373 | (1-70) | (230-650) |
| 3 | 11 | 840 \pm 14 | -31.481 | 28 \pm 7 | 396 \pm 33 |
| | | (766-902) | -64.590 | (0-60) | (210-560) |
| 4 | 8 | 1039 \pm 27 | -31.114 | 12 \pm 5 | 407 \pm 50 |
| | | (950-1168) | -64.450 | (0-35) | (250-620) |
| 5 | 10 | 1060 \pm 12 | -31.493 | 32.4 \pm 8 | 434 \pm 38 |
| | | (985-1121) | -64.665 | (2-80) | (300-700) |
| 6 | 11 | 1224 \pm 12 | -31.338 | 49 \pm 9 | 368 \pm 15 |
| | | (1178-1286) | -64.664 | (5-100) | (300-450) |

We expected fruit ripening phenology to differ within and between elevations; therefore, we visited all seed collection sites on three occasions and only selected a tree when its fruits showed clear signs of maturity (i.e., fruits were brown and dispersed their seeds when blown or shaken). All fruits were collected from 8 to 12 parent trees per site covering the entire crown in January and February 2013. Seeds were dried in ventilated trays under shade and at room temperature (15-25 °C) for 7 days and stored in paper bags at 5 °C until use within the following three months.

To evaluate seed mass and germination proportion for each parent tree, we selected four sub-replicates of 40 seeds, and weighed each seed with a precision of 0.1 mg. The same groups of 40 seeds were then laid on filter paper in Petri dishes, kept moist with deionized water, and checked every 3 days until no more germinations were observed. We used a climate chamber at 15-25 °C

and 12 h night/12 h day, and irrigation as necessary. The temperatures corresponded to the optimum for most native species in the region, according to trials performed for 25 species – albeit not including *Kageneckia* (Funes *et al.*, 2009). Petri dishes were randomly rotated every 3 days to reduce differences in environmental variables within the climate chamber.

To evaluate seedling resistance and/or tolerance to damping-off, total seedling growth and proportional seedling growth during the cold semester, in May 2013 we sowed all the remaining *Kageneckia* seeds in perforated germination trays filled with local soil to a depth of 15 cm in a nursery. The nursery was situated within the distribution range of the target study species at 752 m asl and at 2 km from seed collection site 3 (see Table 1). According to availability, we transplanted 11 to 32 seedlings per parent tree to individual tubes of 28 cm in height and 6 cm in diameter in mid July. We always transplanted seedlings when the first two to three true leaves appeared. All plants were kept in the central area of the nursery and were rotated weekly. We evaluated seedling height (cm) and transplant survival when seedlings were 90 \pm 30 days old and thereafter every 30 days until June 2014 (360 \pm 30 days after emergence date). When a seedling was assessed as dead, we noted the apparent causes including damping-off. Although the evaluation of proportional seedling growth during the cold semester (see data analyses) was not necessary for testing our hypothesis, we included the data because seedlings need to be monitored every 30 days and this metric could be useful to interpret results in relation to a local adaptation hypothesis.

As we were interested in resistance or tolerance to damping-off diseases, we used no fungicides and watered seedlings abundantly when about 30% of the pots presented a dry surface. For ease of manipulation, all plant material was kept on tables under a roof made of transparent polypropylene and a shading fabric which filtered 40% of the sunlight. Hourly temperature in the nursery was recorded using a climatic data logger (Hobo H8) placed 1 m above ground level and under a table.

Data analyses

As estimates of progeny performance, for each parent tree we averaged the following parameters: (1) seed mass (mg-seed⁻¹ as estimated from weighing 4 sub-replicates of 40 seeds), (2) germination (%; $n = 4$ sub-replicates of 40 seeds), (3) seedling survival at the nursery for 360 days (%; $n = 11$ to 32 seedlings); (4) seedling final height at the nursery (cm; $n = 5$ to 23 surviving

seedlings); and, (5) proportional growth during the cold semester calculated as growth from April to September/final height (proportion, $n = 5$ to 23 seedlings). We initially calculated transplant survival (first 90 days) and established seedling survival (last 270 days), but both variables were correlated ($n = 60$ trees; Pearson $R = 0.70$, $P < 0.001$) and showed the same patterns of results; therefore, for simplicity, we integrated both values into one corresponding to the 360 days of monitoring.

Generalized mixed models were used to evaluate effects of elevation, tree height and % rockiness, with progeny averages per parent tree as response variables. Average seed mass, seedling height, and proportional growth in winter were fitted with a Gaussian error distribution using the `lme` function of the `nlme` package in R (R Development Core Team, 2014). Average germination and seedling survival were fitted with binomial error distribution using `glmer` function of the `lme4` package. We considered the progeny average for each parent tree and included site with six levels as random factor. Parent tree elevation, height and % rockiness were included as fixed terms. We checked all residuals for normality and homogeneity assumptions but no transformations were necessary, as expected, because our response variables were averages.

We discarded 9 parent trees with 5 or less seedlings from progeny growth assessment. Thus, we assessed 69 parent trees for seed mass, germination and survival, and 60 parent trees for growth and proportional growth during the cold semester. The statistical analyses performed with all 69 parent trees or only using the 60 parent trees for which we had complete records for all response variables yielded very similar patterns of results; therefore, to facilitate comparisons and the report of results in all analyses we used 60 parent trees throughout the five response variables.

RESULTS

Overall, average (\pm SE) seed mass was 3.09 ± 0.40 mg.seed⁻¹ and average germination proportion in the climate chamber was 0.64 ± 0.01 , with most seeds having germinated after 12 days. In the nursery, survival proportion during the first 360 (± 30) days was 0.58 ± 0.03 .yr⁻¹, and mortality was highest in the first 120 days (Figure 1a). Damping-off was the only detectable cause of mortality throughout the 360 days of monitoring, with aboveground symptoms being the thinning of the stems at ground level and sudden drying up of the plants. Height of the surviving seedlings after the first 360 days averaged 20.1 ± 0.3 cm, with the largest increases in height occurring in the warm semester (Figure 1b and c), with proportional growths of 0.22 and 0.78 for the cold and warm semester, respectively.

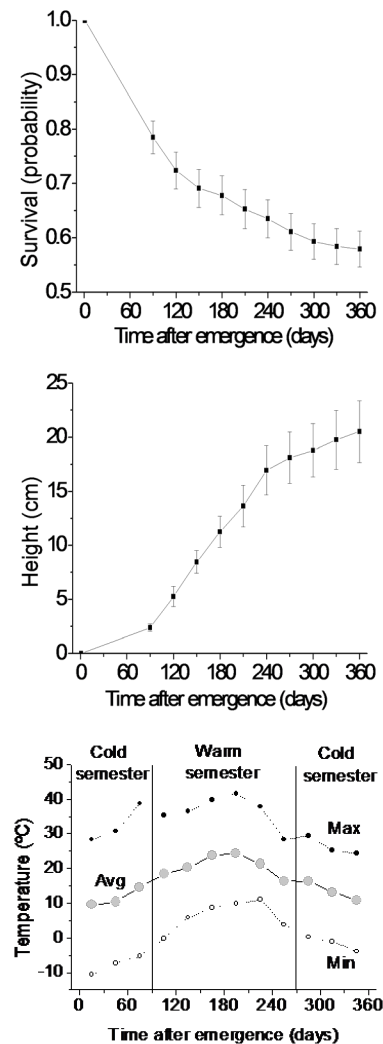


FIGURE 1 (a) Mean survival at a nursery for the progeny of 60 *Kageneckia lanceolata* parent trees (proportion); (b) their height (cm); and (c) Average (Avg), minimum (Min), and maximum (Max) temperature (°C) per 30 day period as recorded at the nursery. We divided with vertical lines the 30- day periods which we considered as the cold and warm semesters.

We found a marked positive relationship between elevation and progeny survival proportion that increased from 0.4 at the lowest collection sites to 0.8 at the highest sites ($p < 0.001$). In addition, we observed a weak positive relationship between elevation and proportional growth during the cold semester, i.e. higher elevation provenances appeared to grow relatively more during the cold semester than the lower elevation provenances ($p = 0.083$). Proportional growth was not related to tree height or rockiness (Table 2, Figure 2). Seed mass, germination and seedling growth were not significantly related to elevation of the parent, tree height or rockiness (GLMM, all p values > 0.05 ; Table 2).

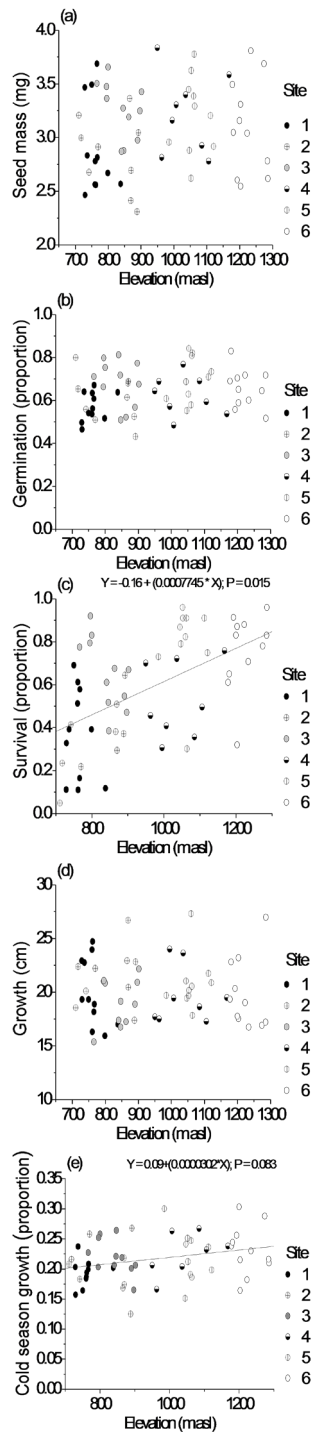


FIGURE 2 Indicators of progeny performance for 60 *Kageneckia lanceolata* as a function of elevation of parent tree. The model and the regression lines are shown for response variables with P values < 0.1. The response variables were averaged per parent tree for: (a) Seed mass (mg-seed⁻¹); (b) Germination in climate chamber (proportion); (c) Average survival of seedlings in a nursery (proportion); (d) Seedling growth (cm-yr⁻¹) at a nursery; and (e) proportion of growth occurred during the cold semester. The six seed collection sites are indicated with different symbols; details of the study sites are provided in Table 1.

TABLE 2 Statistics for generalized linear (t and p) and binomial (z and p) mixed models of five *Kageneckia lanceolata* progeny response variables as a function of elevation of the parent tree, parent tree height and rockiness under the crown (n = 60 parent trees with each parent tree representing the average of its progeny response variable).

| Response variable | R squared | Elevation | Tree height | Rockiness |
|-----------------------|-----------|--------------------------|------------------------|-------------------------|
| 1. Seed mass | 0.018 | t = 0.295 p = 0.770 | t = 0.511 p = 0.612 | t = 0.642 p = 0.524 |
| 2. Germination | 0.029 | z = 1.119 p = 0.263 | z = 0.647 p = 0.517 | z = 0.389 p = 0.697 |
| 3. Survival | 0.288 | z = 4.912 p = < 0.001 | z = 1.077 p = 0.282 | z = 0.453 p = 0.651 |
| 4. Growth | 0.0001 | t = 0.151 p = 0.880 | t = 0.338 p = 0.737 | t = -0.593 p = 0.556 |
| 5. Growth seasonality | 0.075 | t = 1.768 p = 0.083 | t = 0.662 p = 0.511 | t = 0.711 p = 0.481 |

Pearson pair-wise correlations between the five response variables showed weak positive correlations in 4 out of 10 possible cases: seed mass and germination (Pearson r = 0.32; P = 0.014); seed mass and survival (r = 0.31; p = 0.016); germination and survival (r = 0.28; p = 0.048) and survival and proportional growth during the cold semester (r = 0.27; p = 0.037). Seedling growth was the only variable not correlated with any of the others (all p values > 0.05).

DISCUSSION

Our data support the hypothesis that climate at the parent tree site will have a relatively greater influence on progeny resistance or tolerance to pathogens than other indicators of fitness, such as seed mass, germination and seedling growth rate. In our study area, soils are colder and damper at higher elevations (Tecco et al., 2016), which presumably slow germination and extend the time that seeds and germinating seedlings are exposed to pathogens, including those causing damping-off (Tinus and McDonald, 1979). Moreover, especially at lower elevations of the study area, the hotter and drier climate during the past 3000 years (Giorgis et al., 2015 and references therein) may have led to a loss of mechanisms to reduce damping-off in *Kageneckia* seedlings. Variation in soil properties and microbial communities may be an important selective agent to which plants may be locally adapted (Smith et al., 2012). Also in line with a local adaptation explanation is the fact that higher elevation provenances were apparently able to grow proportionally more during the colder semester (albeit this relationship was only marginally significant),

suggesting local altitudinal adaptations. However, further research is still needed to determine whether our results may be explained by local adaptation or other mechanisms such as phenotypic variation transmitted to progeny through maternal seed tissues and without involving nuclear DNA (Vivas et al., 2015).

Indicators of access to soil resources such as rockiness and tree size were not related to any of the five response variables. Several studies report positive relationships between parent tree size and progeny performance (Sletvold, 2002; Renison et al., 2004), and between the amount of resources possibly explored by the parent tree and progeny performance (e.g. Drenovsky and Richards, 2005), whereas other studies found an opposite pattern (e.g. Valfré-Giorello et al., 2012). We suppose that our studied *Kageneckia* parent trees either responds to the amount of resources in other ways, for example, by adjusting the quantity of produced seeds but not their mass, or their access to resources is not indicated by height or rockiness.

The low proportion of the variability explained by our models is in line with local studies in native trees (for *Polylepis australis* Renison et al., 2004; for *Acacia caven* Ashworth and Martí, 2011; for *Sebastiania commersoniana* Valfré-Giorello et al., 2012; and for *Lithraea molleoides*, *Schinopsis marginata*, *Ruprechtia apetala* Torres and Renison, 2017) and may be attributed to influences not evaluated during the present study, such as tree genetic variability, access to high quality pollen, good health of the parent tree, competition with other plants or soil nutrient availability.

We conclude that the pathogenic environment around parental plants could have a great influence on relevant progeny characteristics, such as resistance and tolerance to pathogens, and suggest that incorporating such issues into future progeny studies may yield important findings. More tree species in a wide range of families and situations need to be studied to provide phylogenetic or geographical patterns of resistance and tolerance to pathogens.

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