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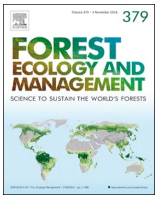

Guiding seed source selection for the production of tropical dry forest trees: *Coulteria platyloba* as study model

Adriana L. Luna-Nieves[a,1], Jorge A. Meave[b,*], Edgar J. González[b], Jorge Cortés-Flores[c], Guillermo Ibarra-Manríquez[a]

[a] *Instituto de Investigaciones en Ecosistemas y Sustentabilidad, Universidad Nacional Autónoma de México, Antigua Carretera a Pátzcuaro 8701, C.P. 58190 Morelia, Michoacán, Mexico*
[b] *Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Coyoacán, 04510 Ciudad de México, Mexico*
[c] *Laboratorio Nacional de Análisis y Síntesis Ecológica, Escuela Nacional de Estudios Superiores, Unidad Morelia, Universidad Nacional Autónoma de México, Antigua Carretera a Pátzcuaro 8701, C.P. 58190 Morelia, Michoacán, Mexico*

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ABSTRACT

A major obstacle faced by reforestation/restoration programs is an insufficient supply of high-quality seed. Seed collection is commonly based on opportunistic strategies that only consider availability and distance to seed sources, but not seed quality. Although for commercial timber species from temperate ecosystems the selection of individuals with above-average phenotypes often results in high-quality seeds and seedlings, the validity of this criterion has not been assessed in tropical dry forests (TDF). By using the abundant TDF tree *Coulteria platyloba* as study model and piecewise structural equation modelling (pSEM), we examined the associations between germination success and seedling growth, and various tree, fruit and seed characteristics, for seeds from two provenances (natural vs. managed populations), that were either scarified or not. Unexpectedly, phenotypic attributes of trees, fruits and seeds had no effect on germination success, as this response variable depended on scarification only. Also, fruit quality was unrelated to tree size, but it was related to provenance. According to pSEM, the best supported path resulting in high quality seedlings established a relationship between managed populations, high quality fruits and seedlings with better roots systems, but only for seeds that were scarified and did not germinate very rapidly. Overall, the assessed relationships were complex, weak, and sometimes difficult to interpret. Nonetheless, these results provide guidance to improve seed source selection efforts that consider operation costs of nurseries and the success of future plantations. In TDF, selecting trees with above-average phenotypes as seed sources does not necessarily favour the quality of seedlings used to restore degraded areas. In these ecosystems, we recommend a seed collection strategy that combines managed and natural populations as seed sources to maximize genetic variability in future plantations, while improving nursery operation efficacy.

1. Introduction

A major operative obstacle faced by nurseries propagating native plant species for reforestation and ecological restoration is an insufficient supply of high-quality seed (Jalonen et al., 2017). This problem is largely related to the criteria guiding seed source selection, which mostly include access to, and availability of, individual trees located near nurseries (Broadhurst et al., 2015; Whittet et al., 2016). Although such opportunistic strategy assumes adaptive advantages in plantations to local climate (Mijnsbrugge et al., 2010), it rarely considers seed quality, an attribute closely related to seed germination success and seedling growth (Gregorio et al., 2015). Eventually, these characteristics will drive success of future plantations (Chirino et al., 2009). Moreover, as seed collection usually concentrates on few individuals, genetic bottlenecks occur that compromise long-term plantation survival due to reduced adaptability to environmental variation in reforested or restored sites (Boshier and Amaral, 2004; Mckay et al., 2005). Such seed collection strategy does not guarantee an adequate seed supply to meet immediate demands, thus rendering harvest size uncertain (Mortlock, 2000; Broadhurst et al., 2008; Mendizábal-

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* Corresponding author at: Circuito Exterior s/n, Coyoacán, C.P. 04510 Ciudad de México, Mexico.
E-mail addresses: adriana.lunan@gmail.com (A.L. Luna-Nieves), jorge.meave@ciencias.unam.mx (J.A. Meave), edgarjgonzalez@ciencias.unam.mx (E.J. González), jcortes@cieco.unam.mx (J. Cortés-Flores), gibarra@cieco.unam.mx (G. Ibarra-Manríquez).

[1] Present address: Departamento de Ecología y Recursos Naturales, Facultad de Ciencias, Universidad Nacional Autónoma de México, Coyoacán, 04510 Ciudad de México, Mexico.

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Hernández et al., 2015).

These problems may be overcome through an alternative strategy that considers maternal effects in selecting high quality seed sources (Smith, 1986; Alba-Landa et al., 2008). Accordingly, a seed tree is selected in a natural population by searching for desired (above-average) phenotypic attributes, such as tree height, stem straightness, or crown width (Jara, 1994; FAO, 2014). The basic tenet is that phenotypic attributes of selected seed trees will be inherited to its progeny, by assuming that its seed has above-average quality (Mesén, 1998). Various studies have provided evidence supporting this notion (Venter and Witkowski, 2011; Kainer et al., 2007); yet, many of them were conducted in temperate regions (Europe, northern North America), while only a few come from tropical or subtropical regions in Asia and Australia. Many of these studies focused on tree species for commercial plantations, and aimed at propagating individuals with dasometric characteristics desirable for timber production (Johnson and Cline, 1991; Jara, 1994). By contrast, selection of high-quality seed sources has been largely overlooked by reforestation and ecological restoration programmes (Pakkad et al., 2003; Jalonen et al., 2017), despite extremely low seedling survival and growth rates often reported in such activities (Mexal et al., 2009; Le et al., 2012, 2014).

Using poor-quality seed is particularly critical in TDF reforestation and restoration programmes (Burdett, 1990). The long dry season typical of these systems (as many as eight months; Murphy and Lugo, 1986) represents a major limitation for seedling establishment and survival (Chirino et al., 2009). Clearly, assessing the extent to which seed source selection focused on best phenotype trees is related to the provision of high-quality seed is important, as this would allow the production of adequate seedlings to be used in land amelioration efforts in these ecosystems. There is a well-known positive association between seed size, germination success and seedling growth (Stanton, 1984; Marshall, 1986, Seiwa, 2000; Metz et al., 2010). Also, the relationship between fruit size and phenotypic attributes of the fruiting tree is well established (Snook et al., 2005; Venter and Witkowski 2011). However, to our knowledge no study focused on native species has examined the potential relationships between tree attributes and the quality of the fruits, seeds, and seedlings that they produce.

In the Mexican dry tropics, *Coulteria platyloba* (S.Watson) N. Zamora, Fabaceae (*frijolillo*), is frequently used in revegetation campaigns, or in implementing agroforestry systems, and thus it is among the most commonly propagated species in nurseries across the region (Luna-Nieves and Ibarra-Manríquez, unpublished). Typically, seed of this species is collected from no more than three individuals in managed populations (trees planted around or near nurseries). The preference for managed populations as seed sources derives not only from easy access to these trees, but also from the assumption that the quality of seed collected from these trees is higher than that of seed whose provenance is the natural populations (natural vegetation remnants). Therefore, our goals were to examine, under nursery conditions, whether seed germination success and seedling quality of *C. platyloba,* both from natural and managed populations, are related to the characteristics of the seeds, fruits and trees from which they originate. As scarification is commonly applied in plant propagation of legumes, we included this factor as it could potentially affect these relationships. Ultimately, our aim was to provide guidelines to improve the criteria to select seed sources for reforestation or ecological restoration programmes in TDF regions.

2. Materials and methods

2.1. Study area and species

This study was conducted in Churumuco, a locality in the lower Balsas River Basin, Michoacán State, southern Mexico (18° 38′–18° 44′ N, 101° 38′–101° 41′ W). Regional climate is tropical (warm), dry, with summer (June-September) rains (BS_0); mean annual temperature is 28 °C and total annual precipitation is 650 mm. TDF is the prevailing vegetation type, with Burseraceae, Cactaceae and Leguminosae being the most diverse plant families; among the latter, *C. platyloba* is a common forest element (Cortés-Flores et al., 2019).

Coulteria platyloba is a typical TDF tree species and endemic to Mexico (Sotuyo et al., 2017). In Churumuco it fructifies just after leaf shed, between October and November (Luna-Nieves et al., 2017). Because of its high-density wood (0.8 g/cm^3) and high resistance to rot (Forster et al., 2002), it is widely used across its range for making poles used in rural home construction, for fencing pastures or crop fields, or as stakes for tutoring crop plants (Rendón-Carmona et al., 2013). Propagating this species under nursery conditions requires pretreatment of its hard coat, highly lignified and impermeable seeds. Scarification breaks physical dormancy of hard coat seeds (Baskin and Baskin, 2004); the most common scarification methods for this species are mechanical (sanding or hot water immersion; Sánchez-Soto et al., 2016).

2.2. Tree selection and phenotypic variation assessment of trees, fruits and seeds

We searched for *C. platyloba* individuals both in natural and managed populations of this species, through extensive surveys in the area. Natural populations were located in the buffer zone of the Zicuirán-Infiernillo Biosphere Reserve, an area of 892 ha along an elevational gradient stretching from 300 to 1200 m a.s.l. By contrast, all individuals from managed populations grew at a lower elevation (200 m), in backyards in Churumuco, around crop fields or pastures, or along roads.

We assessed phenotypic variation among *C. platyloba* individuals from these two provenances by measuring architectonic characteristics of 357 potentially reproductive trees (DBH ≥ 8 cm; Bullock, 1985). For each tree we measured total height, and calculated crown cover (from two perpendicular diameters), and basal area (from DBH). In the case of multi-stemmed trees, we measured each DBH separately and calculated the tree's total basal area by summing the individual basal area values of all stems.

Phenotypic variation among reproductive trees was maximised through a stratified sampling approach based on the distinction of three DBH categories: I, < 20 cm; II, 20–30 cm, and III > 30 cm. For each category we selected 10 individuals from natural populations and five from managed populations ($N_{\text{natural}} = 30$, $N_{\text{managed}} = 15$). Next, we recorded the total number of fruits in each tree's crown, and from each crown we collected 25 fruits lacking insect or pathogen damage ($N_{\text{fruits}} = 1125$). The fruits were stored in paper bags for 15 days at room temperature (~30 °C). We weighed the fruits with an analytical balance and measured their length, width, and thickness with a digital vernier. We recorded the number of seeds and the proportion of healthy seeds per fruit (not immature or malformed and lacking fungal infection or insect predation). Lastly, we randomly selected 25 healthy seeds of each tree, weighed them, and measured their length, width, and thickness ($N_{\text{seeds}} = 1125$).

2.3. Seed germination and seedling growth

Germination assays were conducted in a shade house (80% shade) in the study site. We used polyethylene bags (20 × 15 × 30 cm) filled with local soil. The experiment included a pretreatment with mechanical scarification (sanding with 120 grade sandpaper) and the control (no pretreatment). For each tree from either population, we placed 15 seeds per bag (150 seeds by DBH category; N_{natural}: 15 seeds × 3 categories × 10 trees × 2 pretreatments = 900, N_{managed}: 15 seeds × 3 categories × 5 trees × 2 pretreatments = 450). We watered daily the seeds during 70 days at dawn and dusk and recorded seed germination, as indicated by radicle emergence.

Next, we selected the four seedlings from each tree that germinated first ($N_{\text{natural}} = 120$; $N_{\text{managed}} = 60$) to assess five growth-related

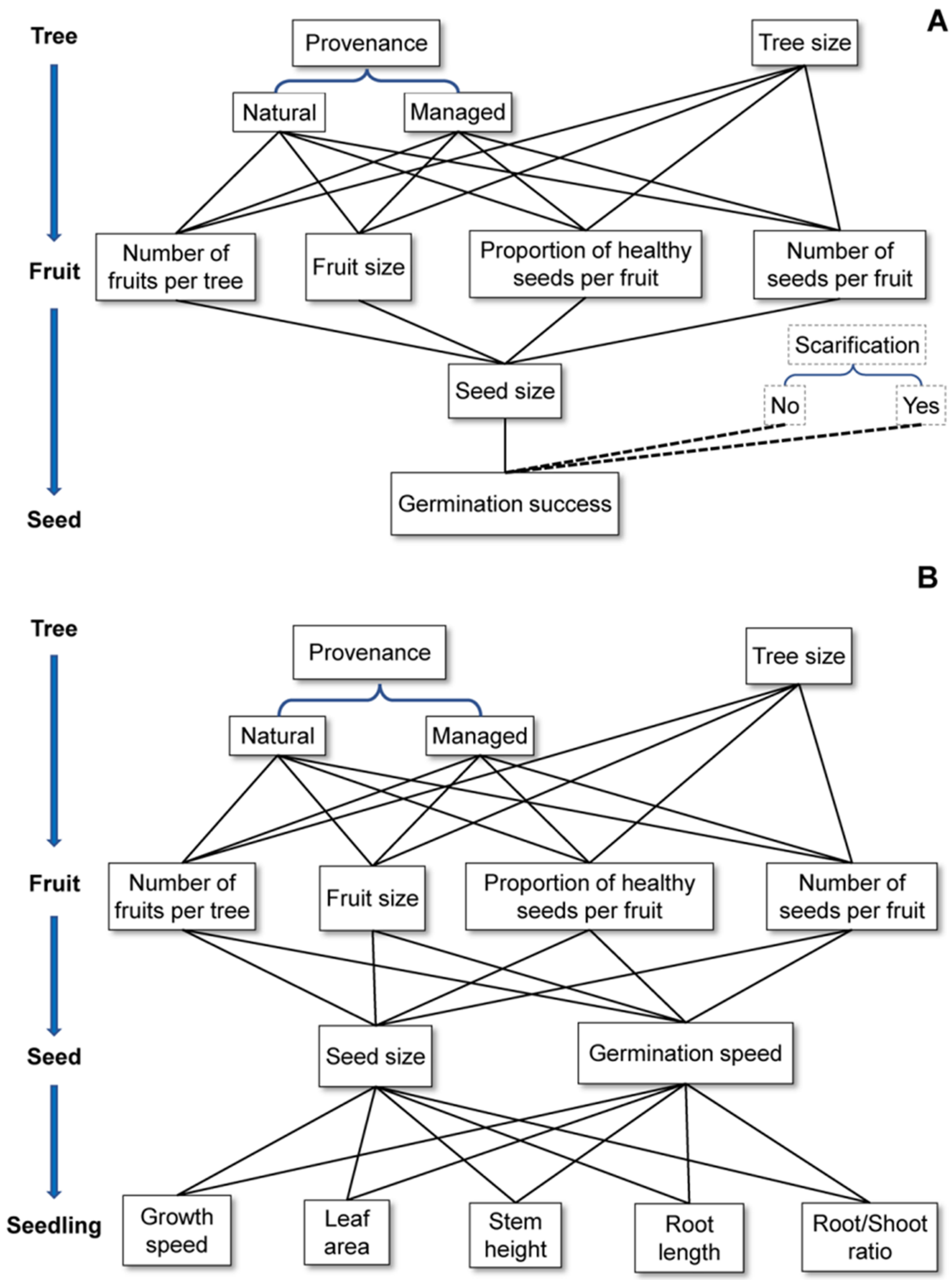

Fig. 1. Conceptual models used to assess whether germination success (A) and seedling growth for either scarified or non-scarified seeds (B) are related to phenotypic characteristics in three stages of *Coulteria platyloba*'s life cycle (tree, fruit, seed). The boxes represent the variables used in the models. Dichotomic variables (Provenance, Scarification) are indicated with horizontal brackets. Scarification is indicated with a broken line to highlight the fact that this variable is not an intrinsic trait of the species' life cycle, but rather an experimental treatment.

variables. Growth speed was defined as the inverse of the time elapsed between germination and the emergence of the first true leaf (carbon uptake initiation in seedlings). Seedlings were harvested when the third true leaf expanded to homogenise ontogenetic stage. We estimated leaf area by analysing leaf photographs with ImageJ (Rueden et al., 2017). For each seedling, we measured stem height (to the highest meristem) and root length, and oven-dried these parts to constant weight to calculate the root/shoot ratio (Hunt, 1982).

2.4. *Statistical analyses*

Given the continuous nature of the four stages examined as part of a tree's life cycle (tree, fruit, seed, seedling), our analysis was based on the construction of three sets of piecewise structural equation models (pSEMs). The first conceptual model allowed us to analyse seed germination success (Fig. 1A), whereas the second one (Fig. 1B) allowed the analysis of seedling growth variables for seedlings derived either from scarified or non-scarified seeds. These probabilistic models connect multiple predictive and response variables in a path diagram with lines indicating which variables influence (or are influenced by) other variables. In pSEMs each path is assessed through the construction of individual models, which are later combined to construct the whole model (Lefcheck, 2016).

Variables used to characterise the tree stage were size and provenance (natural versus managed population). For the fruit stage, we recorded number of fruits per tree, fruit size, number of seeds per fruit, and proportion of healthy seeds per fruit. Seeds were characterised by size and germination speed. Last, seedling growth was described based on growth speed, leaf area, stem height, root length, and root/shoot ratio. Although we measured several tree, fruit and seed morphometric variables, we excluded for the modelling process those with high collinearity ($r > 0.6$); therefore only basal area was used to describe tree size, and weight to define both fruit and seed size. These three variables were selected due to ease and accuracy of measurement associated with them.

We constructed individual models using generalised linear mixed-effect models (GLMMs). These models evaluate the relationships among all possible combinations of explanatory variables with each tree, fruit, seed and seedling response variable, thus creating all possible paths between each pair of levels (i.e., tree-fruit, fruit-seed, seed-seedling). In constructing GLMMs, we considered both models with main effects only and models with interactions. All variables included in the models were transformed to facilitate their fitting (see Table 1 for transformations). After constructing the first set of GLMMs, we noted some counter-intuitive results, which were explained by the data associated with one single tree whose dimensions were well above average; we removed this outlier from the final analyses.

Table 1
Components of each averaged best-supported pSEM examining the relationships between germination success (A), and seedling growth from either non-scarified (B1) or scarified (B2) seeds, with tree, fruit and seed characteristics of *Coulteria platyloba*. Response variables transformations are indicated with a superscript letter; a, $(x–m_x)/S_x$; b, $(\ln(x)–m_{\ln(x)})/S_{\ln(x)}$; c, $(\ln(x+1)–m_{\ln(x+1)})/S_{\ln(x+1)}$; d, logistic($x$). Lower-case letters preceding each equation indicate their graphic representation in Figs. 3 and 4.

Component by response variable	R^2
A. Germination success	
Germination success^{d} (Non-scarified) = −1.71	0.02
Germination success^{d} (Scarified) = 0.73	0.02
B1. Seedling growth in non-scarified seeds	
a. Fruit size^{b} (Natural) = −0.49	
Fruit size^{b} (Managed) = 0.53	0.30
b. Proportion of healthy seeds per fruit^{a} (Natural) = −0.22	
Proportion of healthy seeds per fruit^{a} (Managed) = 0.95	0.04
c. Number of seeds per fruit^{b} (Natural) = −0.21	
Number of seeds per fruit^{b} (Managed) = 0.07	0.02
d. e. f. Germination speed^{c} = −1.36 − 0.01 × Fruit size − 0.05 × Proportion of healthy seeds per fruit^{a} + 0.11 × Number of seeds per fruit^{b}	0.02
g. Growth speed^{b} = −0.52 − 0.39 × Germination speed^{c}	0.09
h. Leaf area^{b} = 0.04 + 0.13 × Germination speed^{c}	0.02
i. Stem height^{b} = −0.68 − 0.34 × Germination speed^{c}	0.09
j. Root length^{b} = 0.15 + 0.35 × Germination speed^{c}	0.09
k. Root/shoot ratio^{a} = 0.14 + 0.32 × Germination speed^{c}	0.09
B2. Seedling growth in scarified seeds	
a. Fruit size^{b} (Natural) = −0.36	
Fruit size^{b} (Managed) = 0.73	0.19
b. Number of seeds per fruit^{c} (Natural) = −0.11	
Number of seeds per fruit^{c} (Managed) = 0.25	0.05
d. f. Germination speed^{c} = 0.65 + 0.03 × Fruit size^{c} + 0.03 × Number of seeds per fruit^{c}	0.02
g. Growth speed^{b} = 0.67 − 0.98 × Germination speed^{c}	0.10
h. Leaf area^{b} = −0.04 + 0.37 × Germination speed^{c}	0.02
i. Stem height^{b} = 0.11 + 0.03 × Germination speed^{c}	< 0.01
j. Root length^{b} = 0.28 − 0.15 × Germination speed^{c}	< 0.01
k. Root/Shoot ratio^{a} = 0.23 − 0.15 × Germination speed^{c}	< 0.01

With the corrected GLMMs we constructed all possible pSEMs, both for germination success and for each seedling growth variable. For each set of models associated with each response variable, we calculated their respective sample-corrected Akaike Information Criteria (AICc), and R^2 values following Nakagawa and Schielzeth (2013). Those pSEMs that differed in less than two AICc units from the pSEM having the smallest AICc were considered to be equally supported and averaged using AICc weights. All analyses were performed in R (R Core Team, 2014) using the AICcmodavg (Mazerolle, 2017), lme4 (Bates et al., 2015) and piecewise SEM (Lefcheck, 2016) packages.

3. Results

3.1. Variation in all life cycle stages of *C. platyloba*

The variation of all phenotypic characteristics assessed in adult trees of *C. platyloba* differed between provenances (Appendix A). Overall, trees from managed populations were taller and had more than twice as many fruits than those from natural populations, even though basal area and crown cover were on average smaller in the former group. In turn, fruits and seeds were slightly larger in trees from managed than from natural populations, according to all assessed morphometric variables. Also, fruits from managed populations had on average more seeds, yet the proportion of healthy seeds was slightly smaller in these populations than in natural ones.

Regarding the seedling stage (Appendix B), scarification emerged as a main factor driving seedling phenotypic variation; seedlings derived from scarified seeds had higher values for all response variables, compared with seedlings from non-scarified seeds. Moreover, final seedling size also differed between provenances: those from managed populations grew more, but did so more slowly than seedlings whose provenance was natural populations (descriptive statistics of this results are given in Appendix B).

3.2. Germination success

Germination success was relatively low, as less than half (40%) of the 1350 seeds used in the study germinated. More importantly, germination success was clearly associated with mechanical scarification; of all germinated seeds, 79% had been scarified, while the remaining 21% were not subjected to this pretreatment. In addition, regardless of pretreatment condition, germination percentage was higher for natural than for managed populations (Fig. 2a), as confirmed by the assessed pSEM (Fig. 2b, c; Table 1). Unexpectedly, none of the several assessed phenotypic characteristics defining the trees, the fruits, or the seeds showed any clear relationship with germination success in this species.

3.3. Seedling growth

While the models used to evaluate the relations among tree, fruit, seed and seedling characteristics produced different paths, all of them shared at least one path, which enabled us to combine them into a single general model (Fig. 3, Table 1, models B1 and B2). According to this model, no single variable describing fruit phenotype was related to tree size, but they were related to tree provenance. Trees from managed populations bore larger fruits (mean weight larger by 0.4 g, Fig. 4a), a larger proportion of healthy seeds per fruit (30% more, Fig. 4b), and a larger number of seeds per fruit (0.5 more seeds, Fig. 4c), compared with trees from natural populations. The number of fruits per tree was not related to any characteristic assessed in adult trees and thus was not included in the general model (Fig. 3).

The relationships between fruit traits and seed size was not clear, but there was a relationship between these traits and seed germination speed. For non-scarified seeds, the relationships between these two sets of variables were extremely weak (Fig. 4d, e); seeds germinated somewhat faster only in the case of fruits containing many seeds (ca.

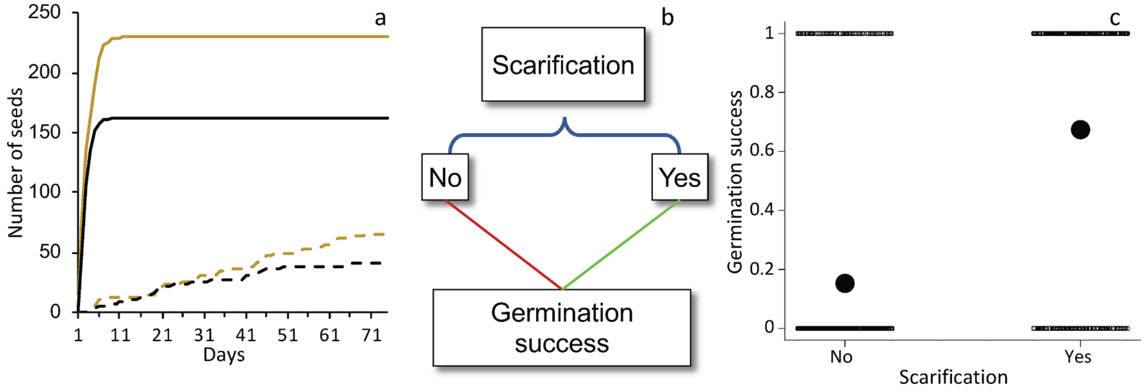

Fig. 2. Germination success of *Coulteria platyloba*. (a) Cumulative germination curves: dashed and solid lines represent non-scarified and scarified seeds, respectively; gold and black lines represent provenance from natural and managed populations, respectively. (b) Best-supported pSEM examining the relationships between germination success and scarification. The red and the green lines indicate a negative and a positive relation, respectively. (c) Graphic representation of the model; its mathematical expression is presented in Table 1(A).

two days faster; Fig. 4f). Conversely, for scarified seeds the relationships between fruits and seed characteristics were clearer; in particular, seeds from both large fruits and fruits bearing more seeds germinated faster (ca. five days earlier; Fig. 4d, f).

Our model also showed that germination speed was differentially related to seedling characteristics, depending on whether seeds had been scarified or not. For non-scarified seeds, the relationships between germination speed and leaf area, root length and root/shoot ratio were positive (Fig. 4h, j, k). By contrast, germination speed showed a negative relationship with growth speed and stem height (Fig. 4g, i). A different scenario emerged for scarified seeds. In this case, a faster germination was associated with a slower seedling growth (Fig. 4g), shorter roots (Fig. 4j), and a smaller root/shoot ratio (Fig. 4k), but with a larger leaf area (Fig. 4h) and taller stems (Fig. 4i).

4. Discussion

Finding guidelines for seed source selection aimed at obtaining high quality seedlings to ameliorate degraded areas remains a big challenge. In this study, we were able to examine the relationships between seedling quality and the phenotypic variation of established plants for an important TDF species, by integrating quantitative attributes assessed at different stages of the life cycle. In doing so, we expected to identify optimal paths to maximise seedling quality. Surprisingly, most relationships were complex and for the most part, weak. Even so, our results shed new light on this problem, which in the case of tropical trees has remained largely ignored.

4.1. Germination success

Contrary to existing evidence for a positive relationship between seed size and germination success (Obeso, 1993; Ouborg and van Treuren, 1995), our results do not support such relationship. This is not surprising when considering the overarching positive effect of scarification on germination success, which overrides any potential effect of seed size on seed germination. This fact largely coincides with the findings of previous studies focused on various species of the same genus (Aranson and Saravia, 1991; Ursulino et al., 2007; Kimura and Islam, 2012; Gehan et al., 2013), all of which share the feature of having hard-coated seeds. Hard coats represent an important

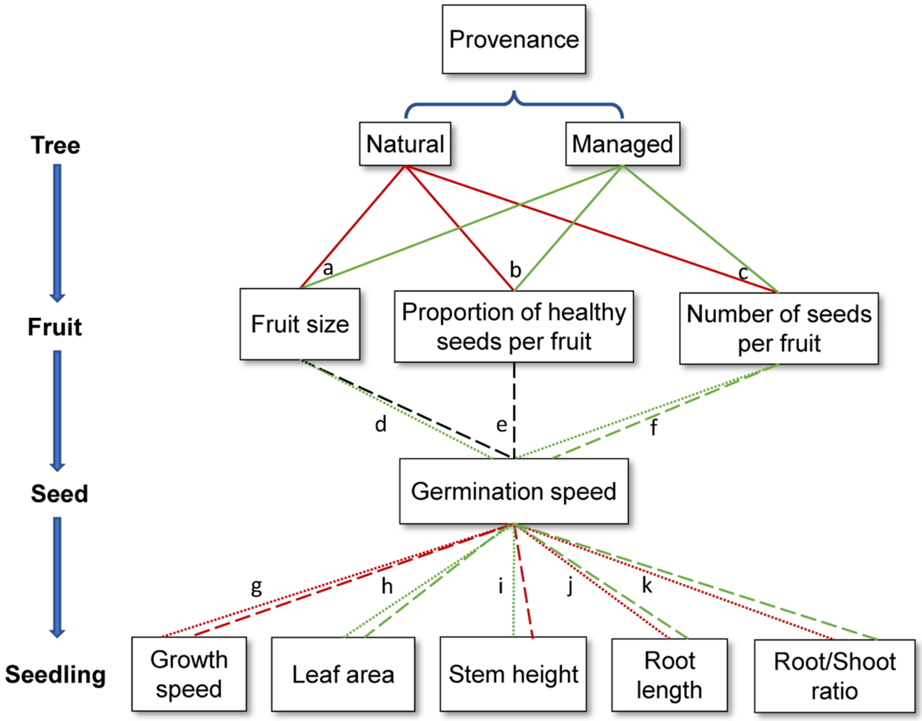

Fig. 3. Average of the best-supported pSEMs constructed to examine the relationships between tree, fruit and seed characteristics of *Coulteria platyloba* and the characteristics of the seedlings they produce, when the seeds were either not scarified (broken lines), or scarified (dotted lines). Red and green lines indicate negative and positive relationships, respectively; black lines indicate ambiguous relationships. The letters indicate the graphic representation of each model shown in Fig. 4. The mathematical expression of each model is shown in Table 1.

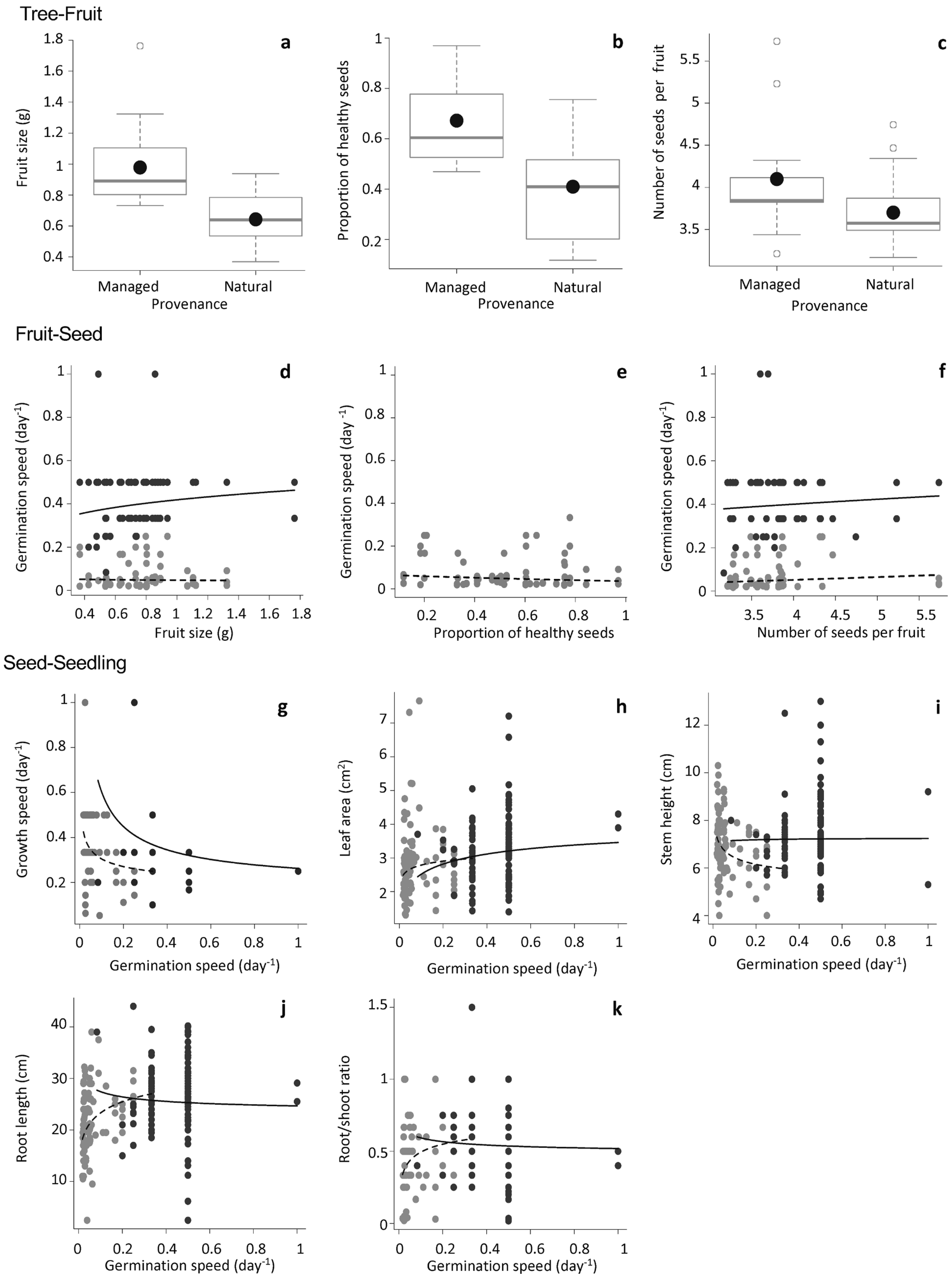

Fig. 4. Graphical representation of the averaged best supported pSEMs constructed to evaluate the relationships between tree, fruit, seed and seedling characteristics of *Coulteria platyloba.* Non-scarified seeds are represented by grey points and dashed lines, while scarified seeds are represented by black points and solid lines. The letter labelling each graph corresponds to the relation evaluated in the general model presented in Fig. 3.

morphological adaptation of seeds in plants living in tropical seasonal environments, as they prevent germination during the long dry period, when survival and growth probabilities are near zero (Lieberman and Li, 1992; McLaren and McDonald, 2003).

4.2. Seedling quality

Some studies have reported relatively larger amounts of xylem and phloem in big than in small trees, which brings about a more efficient nutrient and water delivery for the production of high quality fruits and seeds (Wolfe and Denton, 2001). Against this generalisation, we found that despite the large phenotypic variation displayed by *C. platyloba* trees, tree size was unrelated to any fruit characteristic. Instead, and according to our expectation, provenance showed a clear relationship with fruit quality. Trees from managed populations bore bigger fruits, had more seeds per fruit, and produced seeds that were less predated upon and less affected by pathogens. Such superior fruit quality may be largely explained by the low vegetation density in managed habitats; there, trees usually grow isolated amid crop field or along roads, which likely results in reduced inter-and intra-specific competition (Craine and Dybzinski, 2013) and less frequent herbivore and pathogen attack (Xiao et al., 2017). Likewise, as many of these trees have direct access to water sources, they face smaller hydric stress (Zunzunegui et al., 2010).

Regarding fruit-seed relationships, no single fruit characteristic was related to seed size. Once again, this result disagrees with previous findings that bigger fruits tend to have more seeds per fruit (Janzen, 1982), or contain bigger seeds (Khan et al., 1999). By contrast, higher quality fruits were related to faster-germinating seeds, as long as seeds underwent scarification. Interestingly, however, for non-scarified seeds a higher germination speed resulted in seedlings of higher quality, particularly for those seeds that germinated within ten days from the start of the germination trial (0.5 cm^2 more leaf area, roots that were 10 cm longer, and root/shoot ratio larger by 0.5 units). Although there is no clear explanation to this result, it is likely related to embryo maturation; probably, scarification induces germination when the seed is not yet ready to germinate, which could result in poor quality seedlings. By contrast, non-scarified seeds may commonly germinate when the embryo is mature, and in turn would lead to better quality seedlings.

The situation for scarified seeds is quite the opposite. In this case, those seeds that germinated faster (as early as six days after the star of germination trial) was not associated with better quality seedlings: they grew more slowly (they took as many as 30 days to produce the first true leaf), had shorter roots (4 cm shorter) and a smaller root/shoot ratio, compared to seedlings derived from non-scarified seeds that germinated late. Thus, seedlings produced by rapid-germinating scarified seeds had undesirable attributes for restoration and reforestation programs, especially if these actions are directed at systems with water limitations and high temperatures, such as TDF. In particular, in ecosystems of this kind it is essential that seedlings used in forest rehabilitation efforts have a better-balanced biomass distribution, as reflected by an appropriate root/shoot ratio (Grossnickle, 2012). When this ratio approaches 2, survival of seedlings under field conditions increases considerably (Jaenicke, 1999; Mexal et al., 2009; Nyoka et al., 2018), because they are better able to reach deeper soil horizons and search for soil water more efficiently; also, shorter stems tend to produce fewer leaves, thus reducing transpiration rate (Rincón and Huante, 1993; Haase, 2007; Bayalaet al., 2009; Saboya and Borghetti, 2012).

The integrated assessment of our conceptual model relating different stages of *C. platyloba*'s life cycle revealed various relationships with different directions (i.e., positive or negative) between some tree, fruit and seed attributes with seedling quality, which is the focal input in plant propagation enterprises. Therefore, it is noteworthy that while all models revealed relatively strong relationships between some tree and fruit attributes, the associations between fruit and seed attributes were rather weaker, and even more so the associations between seed and seedling attributes. Such decreasing trend in the strength of these relationships could be due to the combined action of multiple environmental and biological factors with contrasting effects on them. Future studies should attempt to gain new insights on these complex interactions, for example by considering the role of genetic variation and epigenetic effects in seed traits, moreover the different responses among functional groups, as those recognised for TDF trees (Poorter and Markesteijn 2008; Lebrija-Trejos et al., 2010), or the effects of human management.

4.3. Implications for seed source selection

Our results clearly show that selecting seed sources for *C. platyloba* based on above-average tree phenotypes does not guarantee the production of high-quality seedlings under nursery conditions. If *C. platyloba* were an obligate cross-pollinated species, this could be partly attributed to the genetic effect of the father plants; unfortunately, the reproductive system of this species is unknown and our field observations do not help solve this issue. In any case, the lack of strong signals regarding the effect of parental trees brings us back to the initial question as to which attributes of the different stages of the plant's life cycle may serve to guide seed source selection, with the aim of producing adequate seedlings for reforestation/restoration. Although we gathered elements to attempt answering this question, it is obvious that such answer is far from simple. For one, we found that in managed populations fruit quality is higher, but that seeds from this source germinate faster only if scarified. This first result must be connected with the finding that these seeds produce poor quality seedlings, which contrasts with the observation that non-scarified seeds produce seedlings of better quality when they germinate fast. These partly inconsistent results are potentially confusing, as they may lead to thinking that the optimal strategy to produce high quality seedlings should avoid seed scarification. Rather, we contend that in terms of an efficient nursery operation, *C. platyloba* seeds should be scarified, as this action increases germination success. Even though seed scarification entails high costs in human resources, in the long term this practise cuts plant production costs, by reducing the watering period and pre-transplant care, as long as these early differences in seedling traits remain for a longer time than the duration of this experiment.

According to our results, if managed populations are selected as seed sources, it would be advisable to discard seedlings from seeds that germinated very fast, given their high chances to develop inadequate root systems. Yet, we cannot overlook the fact that the difference in seedling quality between natural and managed populations was minimal. Therefore, we may suggest a strategy that combines managed and natural populations as seed sources; selecting either provenance has important consequences regarding nursery operational costs and the success of reforestation/restoration programmes that depend on such seedlings. On the one hand, obtaining seeds from natural populations increases genetic variability in the seedlings used in these programmes, but requires a much larger effort from nurserymen to reach these populations, typically located farther away from the nurseries. Conversely, focusing on managed populations as seed sources reduces time and costs of seed collection, but may result in significant genetic depression, ultimately jeopardizing plantation resilience (Mijnsbrugge et al., 2010). Thus, each strategy's advantages and drawbacks must be carefully pondered in deciding on a particular seed source, in order to maximise benefits both for nurserymen and the reforestation/restoration programmes. Our study highlights the importance of designing specific management plans for the propagation of tree species of interest that integrate the particular biological attributes of the species, along with the specific characteristics of the environment and the idiosyncrasies of the nursery operation.

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Appendix A

See Fig. A1.

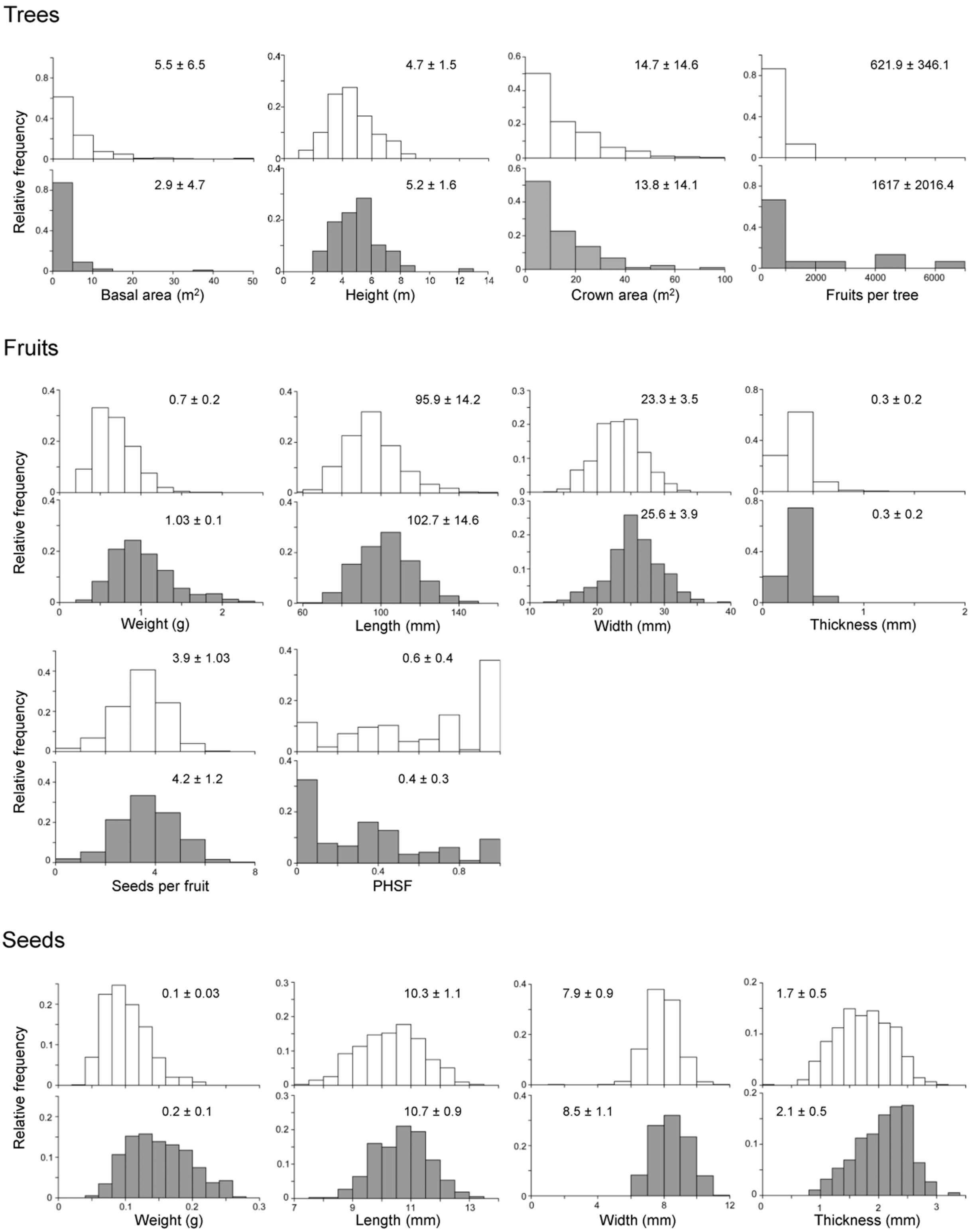

Fig. A1. Histograms of the relative frequency of the phenotypic variation of some characteristics of trees, fruits and seeds of *Coulteria platyloba* in natural (white bars) and managed (gray bars) populations. In each graph the mean and the standard deviation are shown. PHSF = Proportion of healthy seeds per fruit.

Appendix B

See Fig. B1.

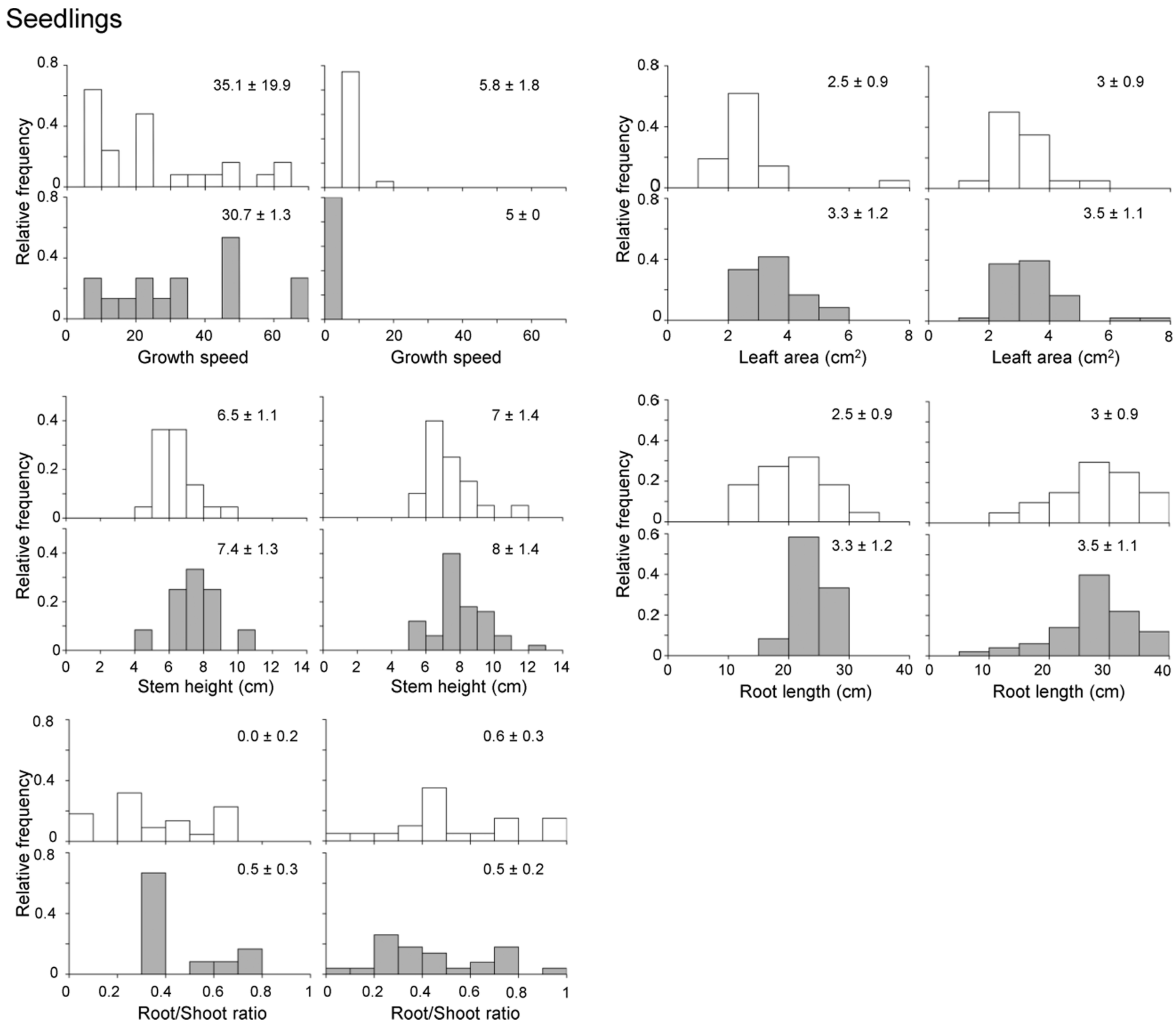

Fig. B1. Histograms of the phenotypic variation of seedlings of *Coulteria platyloba* in natural (white bars) and managed (gray bars) populations. The left and right histograms of each variable represent the non-scarified and scarified seeds, respectively. In each graph is presented the mean and standard deviation.

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