Botany
AMERICAN JOURNAL OF

Seed germination, seedling traits, and seed bank of the tree *Moringa peregrina* (Moringaceae) in a hyper-arid environment[1]

Nasr H. Gomaa[2] and F. Xavier Picó[3,4]

[2]Department of Botany, Faculty of Science, Beni-Suef University, Beni-Suef, Egypt and [3]Departamento de Ecología Integrativa, Estación Biológica de Doñana (EBD), Consejo Superior de Investigaciones Científicas (CSIC), Sevilla, Spain

- *Premise of the study*: Water-limited hot environments are good examples of hyper-aridity. Trees are scarce in these environments but some manage to survive, such as the tree *Moringa peregrina*. Understanding how trees maintain viable populations in extremely arid environments may provide insight into the adaptive mechanisms by which trees cope with extremely arid weather conditions. This understanding is relevant to the current increasing aridity in several regions of the world.
- *Methods*: Seed germination experiments were conducted to assess variation in seed mass, seed germination, and seedling traits of *Moringa peregrina* plants and the correlations among these traits. A seed burial experiment was also designed to study the fate of *M. peregrina* seeds buried at two depths in the soil for two time periods.
- *Key results*: On average, seeds germinated in three days and seedling shoots grew 0.7 cm per day over three weeks. Larger seeds decreased germination time and increased seedling growth rates relative to smaller seeds. Seeds remained quiescent in the soil and germination was very high at both depths and burial times.
- *Conclusions*: The after-ripening time of *Moringa peregrina* seeds is short and seeds germinate quickly after imbibition. Plants of *M. peregrina* may increase in hyper-arid environments from seeds with larger mass, shorter germination times, and faster seedling growth rates. The results also illustrate the adjustment in allocation to seed biomass and correlations among seed and seedling traits that allows *M. peregrina* to be successful in coping with aridity in its environment.

  Key words: aridity; biomass allocation; desert; Egypt; germination; seed mass; trees; unpredictable environments.

Water availability and temperature are two of the main factors that determine the distribution of plants on the land surface (Grace, 1997). Extreme values for these factors pose serious challenges to plants, and can act as powerful selective forces. Hyper-arid areas, characterized by low water availability and high temperatures, are examples of extreme abiotic environments. Rains in hyper-arid environments are infrequent, irregular, and rarely exceed 100 mm. Maximum temperatures can approach 45°C during the hot dry season (FAO Forest Resources Division, 1989). Arid environments occupy almost a third of the total land area of the world and zones classified as hyper-arid cover about 4% of that total (FAO Forest Resources Division, 1989). Recent climatic models predict that aridity will increase in several areas of the world during the 21st century in association with global warming (Seager et al., 2007; Gao and Giorgi, 2008; Solomon et al., 2009). However, study on the processes affecting performance and dynamics of plant populations in hyper-arid environments have received relatively

little attention (but see BenDavid-Novak and Schick, 1997; Bruelheide et al., 2003; Andersen and Krzywinski, 2007; Anthelme et al., 2008; Hegazy et al., 2008; Anthelme and Michalet, 2009). Hence, improving our knowledge of the population biology of plants adapted to extremely arid environments is a matter of utmost importance to better understand and to predict patterns of vegetation change in areas likely to be affected by increasing aridity in the coming decades.

Vegetation in hyper-arid environments is scarce. It tends to be dominated by ephemeral annuals and some perennials, mainly shrubs but also some trees. In hyper-arid regions, trees have important ecological and cultural functions because they represent an element of the landscape that is key to the traditional lifestyle of local human populations (Münzbergová and Ward, 2002; Andersen and Krzywinski, 2007; Abdelrahman and Krzywinski, 2008; Anthelme et al., 2008; Hegazy et al., 2008). There are several traits characteristic of plants in arid environments. For example, trees in such environments strongly depend on groundwater to persist, thus they generally have roots that extend several tens of meters below the surface (Miller et al., 2001; Lubczynski, 2009; Sher et al., 2010). These plants also show physiological adaptations to hyper-arid environments such as increased variability in transpiration and water-use efficiency (Lubczynski, 2009 and references therein). As a result, trees can cope with variation in groundwater availability due to inherent recharge/discharge dynamics that characterize groundwater reserves in such extreme environments (Lubczynski, 2009).

Despite these adaptations, growing in water-limited hot environments has an important demographic drawback, i.e., plants exhibit low fecundity and populations are characterized by very

low recruitment. This can seriously jeopardize long-term population persistence as shown for the trees *Acacia tortilis* (Forrsk.) Hayne [Fabaceae] (Andersen and Krzywinski, 2007; Anthelme and Michalet, 2009), *Balanites aegyptiaca* (L.) Delile [Balanitaceae or Zygophyllaceae] (Andersen and Krzywinski, 2007) or *Moringa peregrina* (Forssk.) Fiori [Moringaceae] (Hegazy et al., 2008) in hyper-arid areas of Niger and Egypt. The demographic stability of long-lived plant populations strictly depends on the survivorship of adult reproductive individuals (García et al., 2008), but no population is viable without effective recruitment of new individuals into the population. For this reason, understanding how trees in hyper-arid areas reproduce and recruit new individuals into the population becomes necessary to evaluate the viability of tree population as a whole.

Recruitment is a demographic process that depends on several factors. One of the most important is seed quality. Seed mass, which is a surrogate of seed quality, strongly influences seedling establishment (Susko and Lovett-Doust, 2000), and variation in seed mass can be affected by developmental constraints, resource limitation, and/or inbreeding depression (Vaughton and Ramsey, 1997 and references therein). Given the generally low fecundity rates observed in trees growing in hyper-arid environments, the quality of the small number of seeds produced can be of paramount importance for recruitment success. In addition, after dispersal seeds need to germinate at the right time to increase the probability of establishment in the population. In hyper-arid areas, where favorable environmental conditions for germination and/or establishment are infrequent and highly unpredictable, accumulating a persistent seed bank may represent a good strategy for buffering the negative impact of a harsh environment on recruitment.

Our study aims to investigate the main biological processes, including seed quality, seedling performance, and seed bank dynamics, all of which may have important implications for recruitment in extremely water-limited hot environments. To this end, we selected the tree *Moringa peregrina*, which occurs in the mountain ranges of the Red Sea region of Egypt, an area of hyper-arid environmental conditions. A earlier field study had indicated that *M. peregrina* exhibits very low fecundity values and extremely low recruitment (Hegazy et al., 2008). Because *M. peregrina* seeds have important economic and medicinal values (Hegazy et al., 2008), increasing our understanding of the species' recruitment patterns is also of interest for the conservation of *M. peregrina* populations. In this study we experimentally evaluate (1) the extent of among- and within-population variation in *M. peregrina* seed mass, (2) the effects of seed mass variation on *M. peregrina* seedling traits including growth and biomass allocation of above- and belowground seedling parts, and (3) the viability of *M. peregrina* seeds buried at various depths in the soil over different time periods. The results are discussed on the basis of their implications to better understand the population dynamics of trees in hyper-arid areas and the adaptive mechanisms by which *M. peregrina* increases recruitment probabilities.

MATERIALS AND METHODS

Plant species and study sites—*Moringa peregrina* is a desert tree (3–10 m height; Fig. 1). This tree has a tuberous rootstock that starts to develop at the seedling stage (Munyanziza and Yongabi, 2007) and exhibits some basal resprouting ability (N. H. Gomaa, personal observation). The leaves have several tiny leaflets that drop when the leaf matures but the naked leaf axes remain. The flowering season spans two months from March to April and the fruiting period

lasts for up to three months (Hegazy et al., 2008). Flowers (10–15 mm long) are generally pinkish white or pale yellow, hermaphrodite, and exhibit insect-pollination syndromes, e.g., large, showy, slightly scented, and zygomorphic. Fruits (10–25 × 1–1.5 cm) are pendulous capsules containing 5–15 ovoid, trigonous, hard-coated seeds (10–19 × 8–12 mm). A trait that characterizes *M. peregrina* populations is reduced fecundity, i.e., the flowering bud withering rate ranges between 40 and 50% and fruit set is extremely low ranging from a low of 0.05 to a high of 0.07% (Hegazy et al., 2008). Large *M. peregrina* trees can produce thousands of flowers but the eventual number of seeds is very low. Resource limitation due to low water availability is assumed to account for this low fecundity (Hegazy et al., 2008).

The distribution of *Moringa peregrina* includes semiarid, arid, and hyper-arid regions of NE Africa (Somalia, Ethiopia, Eritrea, Djibouti, Sudan, and Egypt) and S Middle East (Saudi Arabia, Yemen, and Oman) (Boulos, 1999). In Egypt, *M. peregrina* is restricted to the mountains of the Red Sea region and S Sinai Peninsula. This study was conducted in the mountain ranges of the Red Sea (26°50'N–27°25'N, 33°10'E–33°40'E; approximately 50 km from the Red Sea). The three *M. peregrina* populations in this study are located at similar altitudes (650–700 m a.s.l.) at the base of three different mountains: Gattar, Shayeb El-Banat , and Abu Dukhan. The highest elevations of these mountains are 1963 (Gattar), 2187 (Shayeb El-Banat), and 1705 m (Abu Dukhan). Each population occupies an area of approximately 1500 m^2 and the distance between population pairs ranges from 10 to 25 km. These mountain ranges are traversed by a wadi or gully drainage system, i.e., streambeds that are dry except after a rain. Wadis may receive additional runoff water from the neighboring uplands of their watersheds. This allows for the establishment of plant communities that may receive more water than that given by actual rainfall (Kassas, 1953; Millington and Pye, 1994), although that is difficult to quantify.

The region where the populations are located is typically characterized by a hyper-arid climate. Based on Egyptian meteorological records (Ministry of Civil Aviation, 1975), the annual rainfall in the study area is ca. 4 mm with the rainy season from October to May (on average 0.45 mm rainfall per month). The mean monthly air temperature ranges from 15.7°C in January to 30.0°C in August with a mean annual temperature of 23.2°C. The mean monthly relative humidity varies from a low of 43% in June to a high of 55% in October with a mean annual relative humidity of 49.3%. In the region of study, *Moringa peregrina* is found primarily on rocky slopes of wadis (Fig. 1). Codominant shrubs are *Launaea spinosa* (Forssk.) Sch.Bip. ex Kuntze [Asteraceae], *Zilla spinosa* (L.) Prantl [Brassicaceae], and *Zygophyllum coccineum* L. [Zygophyllaceae]. Other representative shrub species of the plant community include *Aerva javanica* (Burm. f.) Juss. ex Schult. [Amaranthaceae], *Capparis spinosa* L. [Capparidaceae], *Artemisia judaica* L. [Asteraceae], *Fagonia mollis* Delile [Zygophyllaceae], and *Cleome droserifolia* (Forssk.) Delile [Capparidaceae].

Population sampling and experimental design—In late July 2008, a total of 15 adult *Moringa peregrina* trees were randomly chosen in each study population. Target trees in each population were separated 8–15 m from each other. Tree size was determined as the volume of an inverted cone as $V = \pi \times r^2 \times h/3$, where r is the crown radius and h is tree height. Total seed production of an individual tree was estimated as the number of fruits multiplied by the average number of seeds per fruit.

For each tree we collected 4–20 fruits depending on total fruit availability. Seeds were pooled and sets of 40 seeds per individual were used to conduct a germination experiment in a garden in Beni-Suef city (29°5'N, 31°6'E; 30 m a.s.l.; approximately 400 km away from the study sites; mean monthly air temperature of 12.2°C in January and 28.9°C in August; and total annual rainfall of 7.8 mm). In August 2008 soon after harvesting, seeds were individually identified and weighed to the nearest 0.1 mg with a BL-410-S digital balance (Setra Systems, Boxborough, Massachusetts, USA). To test germination, seeds were individually sown in pots (10 × 10 cm) filled with soil collected at the respective study sites (N = 1800 seeds; 3 populations × 15 trees per population × 40 seeds per tree). Pots were randomly set out in the open air but sheltered from direct sun. Pots were given 250 mm water after sowing followed by 100 mm added every two days throughout the duration of the experiment. This amount is by far much more water than a seed would receive under field conditions, but we attempted to avoid the effects of water limitation on seed germination, seedling survival, and growth. We also assumed that lower amounts of water may alter the results, but the goal of this experiment was to assess potential for seeds to germinate and the potential seedling performance of *Moringa peregrina* while minimizing seed and seedling mortality due to undesired external factors. Germination, recorded as the time of emergence of the radicle, was monitored daily for three weeks, so for each seed we obtained the number of days to germination. At the end of the experiment seedlings were carefully unearthed and

Fig. 1.   Photograph of a *Moringa peregrina* population in a mountain wadi from the Egyptian Red Sea region.

washed, shoot and root length were measured for all seedlings, and shoot dry weight and root dry weight were measured after drying at 70°C for two days. For each seedling, the root : shoot ratio, i.e., root dry weight / shoot dry weight, was also calculated.

In early August 2008, we conducted seed burial experiments to study performance of seeds buried in the soil in field conditions. The seed burial experiments included two depth treatments and two time treatments to characterize the spatial and temporal components of seed banks. Normally, seeds easily fall into cracks in the soil so seed density can vary with depth, and seed cohorts become depleted over time due to germination and seed mortality. For each population, we collected 100 seeds from 10 individuals from each population ($N = 3000$ seeds; 3 populations × 10 trees per population × 100 seeds per tree). For each individual, four groups of 25 seeds each were placed in nylon mesh bags. Two bags were buried at 5 cm and the other two at a 20 cm depth, following the range of depths normally found in the literature. Previous field observations also indicated that up to 90% of *Moringa peregrina* seeds can be found at about the first five cm of the soil layer, whereas the remaining 10% are present between 5 and 20 cm depth (N. H. Gomaa, personal observation). Each group of four bags corresponding to each individual was buried with even spacing of 1 m between them. We retrieved one bag per individual and depth combination after 6 and 12 mo after burial in each population of study. These two time periods were selected to monitor seed viability and germination within the first year after seed dispersal and we assume that *M. peregrina* seed viability and germination decreases over time, although *M. peregrina* seeds can be viable up to several years (N. H. Gomaa, personal observation). After retrieval, seeds were immediately placed in plastic bags and brought to the laboratory for the germination assays. Seeds were then placed in moist petri dishes and transferred to an NO : G150 incubator (Biotech Co. for Medical & Laboratory Equipment, Cairo, Egypt) in the Department of Botany at the Faculty of Science at Beni-Suef University. The experiment was conducted in total darkness to simulate the response of buried seeds to a rain episode. Germination was conducted under the optimal range of temperatures for germination observed in this species (30°C : 16 h : day; 20°C : 8 h : night). Germination was recorded every day for 10 days.

Statistical analyses—For each population the relationships among tree size, total seed production, and mean seed mass were analyzed with linear regression models. The random effect of population and the random effect of individuals nested within population on days to germination, shoot length, root length, shoot dry weight, root dry weight, and root : shoot ratio were analyzed with general linear models. Individual seed mass was included as a covariate in these

analyses. Population was considered as random because it represents a random subsample of all *Moringa peregrina* populations available in the area. Pearson's correlation coefficients between pairs of seedling traits were computed using individual mean values for each population of study. The effects of time, population, and depth on the proportion of germinating seeds were analyzed with a three-way repeated measures general linear model in which time was the repeated measure factor with values of 6 and 12 mo. When necessary, variables were transformed for normality, homoscedasticity, and linearity, using arcsine transformation for proportions and log transformation for all other values. Statistical analyses were performed using SPSS v.13 statistical software (SPSS, Chicago, Illinois, USA).

RESULTS

In the study area, the height of *Moringa peregrina* trees ranged from 2.5 to 10 m, whereas their crown radius ranged from 1.25 to 4.5 m. In the study populations, the fruits per tree varied between 1 and 100 fruits and the estimated number of seeds produced per tree varied between 8 and 1000 seeds. Tree size was significantly positively correlated with seed production ($N = 15$, $r > 0.64$, $P < 0.001$ in all populations). In contrast, neither tree size nor seed production were significantly correlated with mean seed mass ($P > 0.05$ in all populations). Seed mass significantly differed among populations ($F_{2,42} = 3.40$, $P = 0.043$) and among individuals within populations ($F_{42,1706} = 8.88$, $P = <0.0001$). On average, mean ± SE seed mass ranged between 0.56 ± 0.01 (Gattar population) and 0.62 ± 0.01 g (Shayeb El-Banat population).

The experiment to analyze the patterns of among- and within-population variation in days to germination and seedling traits indicated that seed mass significantly affected all traits of study except the root : shoot ratio (Table 1). In particular, seed mass was significantly positively correlated with shoot length, root length, shoot dry weight, and root dry weight (all individuals pooled, $N = 45$, $r > 0.63$, $P < 0.0001$ in all cases). In contrast, seed mass was significantly negatively correlated with days to

TABLE 1.   General linear model testing for the effects of population (Gattar, Shayeb El-Banat, and Abu Dukhan) and individuals nested within populations (15 individuals per population) on days to germination, shoot length, root length, shoot dry weight, root dry weight, and root : shoot ratio of *Moringa peregrina*. Individual seed mass was used as a covariate. *F*-values are indicated. Means ±SE are also given for each population of study. Degrees of freedom for all variables: Seed mass (SM), 1; Population (P), 2; Individual (I), 42; SM × P, 2; SM × I, 14; Error, 1689.

	Days to germination	Shoot length (cm)	Root length (cm)	Shoot dry weight (mg)	Root dry weight (mg)	Root : shoot ratio
Factor	*F*	*F*	*F*	*F*	*F*	*F*
Seed mass (SM)	306.2 ***	1149.6 ***	697.1 ***	737.8 ***	556.2 ***	2.3 *ns*
Population (P)	2.2 *ns*	2.0 *ns*	6.7 **	6.1 **	0.3 *ns*	36.4 ***
Individual (I)	1.0 *ns*	4.1 ***	4.4 ***	4.3 ***	3.5 ***	2.2 ***
SM × P	2.0 *ns*	6.5 **	9.4 ***	3.9 *	5.7 **	1.9 *ns*
SM × I	1.7 *ns*	1.5 *ns*	2.1 *	2.0 *	1.9 *	1.7 *
Population	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ± SE	Mean ±SE
Gattar	3.14 ± 0.08	13.8 ± 0.23	3.6 ± 0.05	97.3 ± 2.16	63.5 ± 1.37	0.655 ± 0.003
Shayeb El-Banat	3.04 ± 0.09	15.0 ± 0.22	3.9 ± 0.05	108.9 ± 2.93	61.3 ± 1.74	0.565 ± 0.005
Abu Dukhan	3.01 ± 0.05	14.0 ± 0.20	3.8 ± 0.04	99.7 ± 1.97	63.1 ± 1.60	0.635 ± 0.005

Notes: Significance: ***, $P < 0.0001$; **, $P < 0.01$; *, $P < 0.05$; *ns*, nonsignificant.

germination ($N = 45$, $r > -0.74$, $P < 0.0001$). The effect of population was significant for root length, shoot dry weight and root : shoot ratio (Table 1). The effect of individual was significant for all variables except for days to germination (Table 1). A total of 97.3% of *Moringa peregrina* seeds germinated after three weeks. All seeds germinated between days 2 and 9 (overall mean ± SE = 3.1 ± 0.04 d; Table 1). On average, shoot length after three weeks was 3.8 times larger than root length (Table 1) and shoot dry weight was 1.7 times heavier than root dry weight (Table 1). On average the root : shoot ratio was 0.62 ± 0.006 (Table 1).

The effect of seed mass significantly differed among populations for all variables except for days to germination and the root : shoot ratio (Table 1). This significant seed mass × population interaction was explained by the nonsignificant relationship between seed mass and some variables ($P > 0.061$; root length, shoot dry weight, root : shoot ratio), or by a significant relationship but with a smoother slope between seed mass and some other variables ($r < 0.55$, $P > 0.024$; shoot length, root dry weight) in the Shayeb El-Banat population. Finally, the effects of seed mass on root length, root dry weight, shoot dry weight, and the root : shoot ratio significantly differed among individuals (the seed mass × individual interaction; Table 1) due to the lack of relationship between seed mass and these variables in some individuals of each population (results not shown).

As expected, shoot length, root length, shoot dry weight, and root dry weight were strongly positively correlated among each other in all populations ($r > 0.88$, $P < 0.0001$ in all cases). Days to germination was significantly negatively correlated with shoot length in all three populations (Table 2). The correlation between days to germination and root length, shoot dry weight, and root dry weight showed inconsistent patterns of variation among populations (Table 2). The correlation between days to germination and the root : shoot ratio was not significant in any population of study (Table 2).

The experiment to test germination rate of seeds buried at two depths for 6 and 12 mo indicated that seed germination was significantly affected by retrieval time, population, and depth (Table 3). None of the interactions were significant (Table 3). Seed germination was very high in all treatment combinations but significantly decreased over time (overall mean ± SE = 94.3 ± 0.42 and 91.9 ± 0.57% for 6 and 12 mo after burial, respectively; Fig. 2A). Seed germination was significantly higher at 20 than at 5 cm depth (overall mean ± SE = 90.8 ± 0.49 and 95.5 ± 0.35% for 5 and 20 cm depth, respectively; Fig. 2B).

DISCUSSION

Previous studies indicated that populations of the tree *Moringa peregrina* occurring in the wadis in the mountains of the Red Sea region of Egypt exhibit reduced fecundity and sporadic recruitment due to the severity of the environment (Hegazy et al., 2008). In addition, the demographic effects of such naturally low fecundity and recruitment rates are made worse by the economic and medicinal importance of seeds that are overexploited in the NW sector of the Red Sea area in Egypt (Hegazy et al., 2008). Although *M. peregrina* has the ability to basally resprout, the plant does not reproduce clonally and the long-term persistence of populations totally depends on recruitment, as shown for other long-lived nonclonal plant species exhibiting low recruitment rates (García et al., 1999; Castro et al., 1999; Picó and Riba, 2002; García et al., 2008). Hence, fecundity and recruitment represent key life-cycle phases necessary to maintain viable populations in a species with an estimated generation time of approximately 50–70 yr (Hegazy et al., 2008).

The results show that tree size in *Moringa peregrina* influences seed production, i.e., larger trees produce more seeds, but does not affect mean seed mass. This result suggests that *M. peregrina* appears to favor seed quality over seed number. Theory also predicts that in perennial plants resource investment per offspring tends to be higher in harsh environments (Charlesworth and Morgan, 1991). This seems to be the case for *M. peregrina*, i.e., the severity of the hyper-arid environment is considered the main factor accounting for the observed massive flower abortion rate (Hegazy et al., 2008), so that available

TABLE 2.   Correlation coefficients between days to germination and seedling traits of *Moringa peregrina* for each population of study. Sample size is 15 individuals for each population and correlations were based on individual mean values.

Seedling trait	Gattar	Shayeb El-Banat	Abu Dukhan
Shoot length	−0.60 *	−0.53 *	−0.63 *
Root length	−0.50 *ns*	−0.48 *ns*	−0.61 *
Shoot dry weight	−0.64 *	−0.42 *ns*	−0.50 *ns*
Root dry weight	−0.73 **	−0.48 *ns*	−0.50 *ns*
Root : shoot ratio	−0.32 *ns*	−0.24 *ns*	−0.41 *ns*

Notes: Significance: ***, $P < 0.0001$; **, $P < 0.01$; *, $P < 0.05$; *ns*, nonsignificant.

TABLE 3. Repeated measures general linear model testing for the effects of time (6 and 12 mo after burial), population (Gattar, Shayeb El-Banat, and Abu Dukhan) and depth (5 and 20 cm) on the proportion of germinating seeds of *Moringa peregrina* buried in the soil. Degrees of freedom (*df*) and *F*-values are given.

Factor	*df*	*F*
Time (T)	1	14.6 ***
Population (P)	2	4.3 *
Depth (D)	1	46.3 ***
T × P	2	0.06 *ns*
T × D	1	0.80 *ns*
P × D	2	0.02 *ns*
T × P × D	2	0.20 *ns*
Error	48	

Notes: Significance: ***, $P < 0.0001$; **, $P < 0.01$; *, $P < 0.05$; *ns*, nonsignificant.

Fig. 2. Percent germination obtained from the seed burial experiments for each population (A) and depth (B) buried for 6 and 12 mo.

resources can be fully allocated to the seeds eventually produced. It must be emphasized that more than 97% of the seeds collected for this study germinated under optimal conditions, thus almost all seeds produced by *M. peregrina* trees are viable.

The quality of the seeds produced has a very strong effect on several important seedling traits of *Moringa peregrina*. In general, larger seeds significantly reduce germination time and significantly increase seedling size. This is a common result found in plant biology (Kalisz, 1989; Montalvo, 1994; Helenurm and Schaal, 1996; Galloway, 2001; Picó et al., 2003) highlighting the fact that seed size, which represents one of the earliest traits on which maternal effects are expressed (Roach and Wulff, 1987), may have important consequences for plant fitness as a whole. Furthermore, days to germination and shoot length were significantly negatively correlated in all populations of study, indicating that seed mass, seed germination, and seedling growth are tightly related in *M. peregrina*. The strong consistency of these results among *M. peregrina* populations suggests that germinating quickly, i.e., on average three days to germinate, and growing fast, i.e., on average 0.7 cm of shoot elongation per day over three weeks, could increase the probability of successful seedling/juvenile establishment. As a result, these traits and their tight correlation might be under strong selection in hyper-arid environments.

After three weeks of seedling growth, shoots were almost four times longer on average than roots and twice as heavy. The relationships between the above- and belowground parts of the seedling were highly conserved among all *Moringa peregrina* populations. The same pattern has also been observed in seedlings of other tree species occurring in arid or semiarid areas, such as *Acacia senegal* (L.) Willd. [Fabaceae] in Sudan (Raddad 2007), *Acacia tortilis* (Forrsk.) Hayne [Fabaceae], or *Faidherbia albida* (Delile) A. Chev. [Fabaceae] in N Kenya (Stave et al., 2005) in experiments in controlled conditions without water limitation. It must be emphasized that all these experiments may not reflect what happens under field conditions. Water availability can modify the relationship between above- and belowground biomass (see Stave et al., 2005). However, all these experiments clearly show important consistent differences between root and shoot growth patterns for different tree species, which might be the result of an adaptation to their arid environments. This hypothesis is supported by recent experimental results indicating that greater aboveground growth significantly increases seedling and juvenile survival in *Prosopis africana*
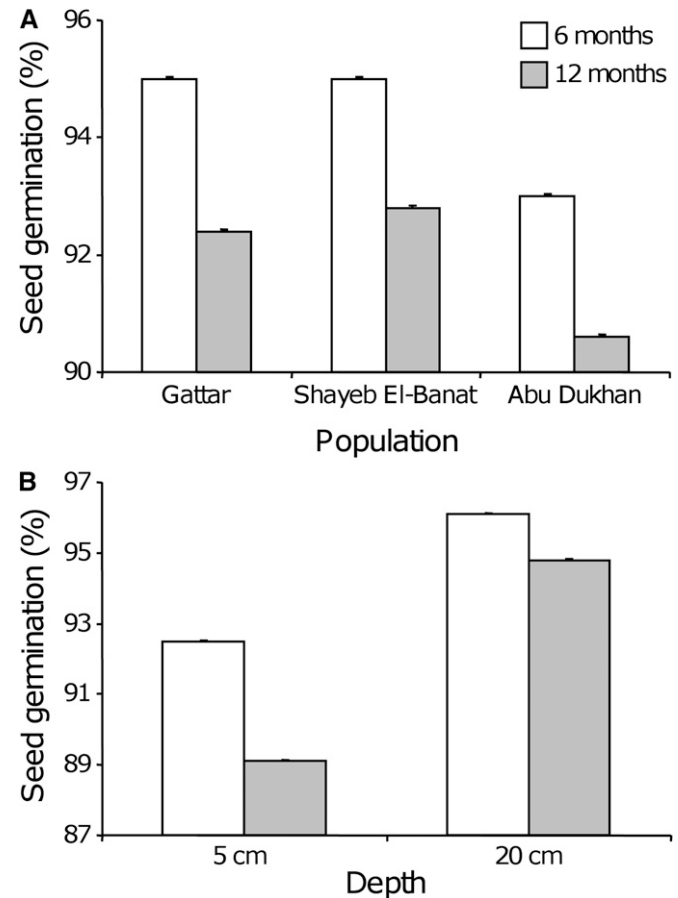
(Guill. & Perr.) Taub. [Fabaceae] in Niger (Weber et al., 2008). Furthermore, the effects of aboveground growth on survival are more important as the environments become drier, a result that is also interpreted as an adaptation to arid conditions (Weber et al., 2008).

Aboveground growth strongly depends on the effectiveness of the root system to access soil moisture due to deeper root development or the ability of roots to store water and nutrients that can be used by the plant. In the case of *Moringa peregrina*, it has been reported that the species can also grow on nearly bare rock, which can be explained by the tuberous rootstock that the plant develops (Munyanziza and Yongabi, 2007). We hypothesize that the tuberous rootstock is a very important structure for the establishment and development of young *M. peregrina* plants. After securing establishment, roots might also expand and elongate to access deeper water supplies that would be necessary to maintain adult *M. peregrina* trees.

Other studies on seed germination requirements of woody species exhibiting hard seed coats in arid areas indicated that acid or mechanical scarification treatments improved germination, as in *Acacia tortilis*, *A. senegal*, *A. seyal* Delile [Fabaceae], and *Dichrostacys cinerea* (L.) Wight & Arn. [Fabaceae] in Ethiopia (but see *Balanites aegyptiaca*; Argaw et al., 1999). This seems not to be the case for *Moringa peregrina*, as our study reveals that *M. peregrina* seeds germinate very fast without any damage to the seed coat. In addition, burial time and

burial depth had only a small but significant effect on seed germination. *M. peregrina* seeds had significantly decreased germination rate over time and seeds buried at 5 cm exhibited significant lower germination rates than those buried at 20 cm. Possible explanations include: (1) seeds have reduced viability over time; (2) higher temperatures at five cm could slightly induce secondary seed dormancy; or (3) the reduced environmental fluctuations experienced at 20 cm could enhance seed viability. In any case, *M. peregrina* seeds maintain very high germination rates among populations, between depths and over time. Overall, these results indicate that *M. peregrina* seeds can remain quiescent in the soil until conditions are right for germination. Our data show that germination rates are high immediately after being dispersed and after one year buried in the soil. In addition, seeds possess the means to react very quickly after imbibition, so seed after-ripening in this species can be quite short. As a matter of fact, the time elapsed between seed harvesting and the seed germination experiment was about a month. The low mortality and high germination rate of seeds buried in the soil might represent a mechanism to buffer the demographic effects of reduced fecundity and recruitment through the accumulation of sound seeds in the soil that remain quiescent while environmental conditions are not conducive for germination. Populations could experience punctual recruitment peaks when environmental conditions turn favorable for seed germination and seedling establishment. However, recent demographic studies on *M. peregrina* in the study area indicate that populations have a weak seed bank (range of estimated seed density in the soil: 0.12–0.50 seeds/m^2; Hegazy et al., 2008) and are exhibiting an overall declining trend (intrinsic rates of increase varying from a low of −0.081 to a high of −0.012; Hegazy et al., 2008). The important post dispersal seed predation by wild and domestic animals and the collection of seeds by local people for medicinal and commercial purposes recorded in the study area seem to account for these results (Hegazy et al., 2008).

The exact combination of environmental conditions that a seedling has to encounter to establish in the population are not known, but the "windows of opportunity" (Eriksson and Fröborg, 1996) for recruitment of *Moringa peregrina* could be as unpredictable and rare as the amount and duration of rain episodes in the area. If aridity increases as predicted in many areas of the world during the 21st century (Seager et al., 2007; Gao and Giorgi, 2008; Solomon et al., 2009), several woody plant species will have to face a harsher environment that is likely to affect several plant features including the distribution, the relative representation of species in the plant community, and/or different plant fitness components. For instance, paleoecological studies spanning the last 10000 yrs in S Iberian Peninsula indicate a replacement of tree species as a result of temporal changes in temperature and moisture conditions in the area (Carrión et al., 2001). In addition, recent studies that experimentally manipulated the climate of a plant community show that increasing drought and temperature induce discrepancies between recruitment and the adult performance, which can lead to shifts in community composition as a whole (Lloret et al., 2009). Finally, aridity also seems to be an important factor in plant evolution that may accelerate evolutionary rates of traits that enable plants to withstand periods of severe drought (Stebbins, 1952; Axelrod, 1972).

The *Moringa peregrina* populations chosen in this study represented a random selection of populations located at the same altitude to minimize the effects of altitude-mediated environ-

mental variability on trees. However, we have detected a significant population effect on many *M. peregrina* seed and seedling parameters analyzed in this study. This suggests that *M. peregrina* populations have some characteristics that make them different from each other. Water availability in wadis is the most important limiting factor for plant population performance. Water sources include both episodic rain and runoff water from neighboring uplands of the wadi watersheds. We suggest that physical differences among watersheds influence the total amount of water available for *M. peregrina* trees in each population of study, which could account for the among-population variation found in this study.

How can the results of this study based on the tree *Moringa peregrina* growing in water-limited hot environments increase our understanding of the effects of the predicted increasing aridity on tree species in several areas of the world? It is clear that aridity reduces overall fecundity and recruitment that in turn represent key life-cycle phases for the long-term maintenance of tree populations. Based on our present results in conjunction with past research on *M. peregrina*, we conclude that the strategy adopted by *M. peregrina* to survive in its hyper-arid environment is the following: (1) adjustment of resource allocation to the reduced number of seeds eventually produced to increase seed quality; (2) reduction of germination time and increase of seedling growth rates once water is available, which are all mediated by seed size. The tight correlation among these traits found in this study can be interpreted as a mechanism to react quickly to the unpredictable rains; and (3) accumulation of a quiescent seed bank whose seeds are ready to germinate right after imbibition. Although the patterns found in this study may not be applicable to other tree species due to different reasons, e.g., phylogenetic or developmental constraints, *M. peregrina* represents a good example of successful adaptation to extremely arid environments from which several lessons can be learned.

LITERATURE CITED

ABDELRAHMAN, H. F., AND K. KRZYWINSKI. 2008. Environmental effects on morphology of *Acacia tortilis* group in the Red Sea Hills, North-Eastern Sudan and South-Eastern Egypt. *Forest Ecology and Management* 255: 254–263.

ANDERSEN, G. L., AND K. KRZYWINSKI. 2007. Mortality, recruitment and change of desert tree in a hyper-arid environment. *PLoS ONE* 2: e208.

ANTHELME, F., A. ABDOULKADER, AND G. BESNARD. 2008. Distribution, shape and clonal growth of the rare endemic tree *Olea europaea* subsp. *laperrinei* (Oleaceae) in the Saharan mountains of Niger. *Plant Ecology* 198: 73–87.

ANTHELME, F., AND R. MICHALET. 2009. Grass-to-tree facilitation in an arid grazed environment (Aïr Mountains, Sahara). *Basic and Applied Ecology* 10: 437–446.

ARGAW, M., D. TEKETAY, AND M. OLSSON. 1999. Soil seed flora, germination and regeneration pattern of woody species in an *Acacia* woodland of the Rift Valley in Ethiopia. *Journal of Arid Environments* 43: 411–435.

AXELROD, D. I. 1972. Edaphic aridity as a factor in angiosperm evolution. *American Naturalist* 106: 311–320.

BENDAVID-NOVAK, H., AND A. P. SCHICK. 1997. The response of *Acacia* tree population on small alluvial fans to changes in the hydrological regime: Southern Negev Desert, Israel. *Catena* 29: 341–351.

BOULOS, L. 1999. Flora of Egypt. Al Hadara Publishing, Cairo, Egypt.

BRUELHEIDE, H., U. JANDT, D. GRIES, F. M. THOMAS, A. FOETZKI, A. BUERKERT, W. GANG, ET AL. 2003. Vegetation changes in a river oasis on the southern rim of the Taklamakan Desert in China between 1956 and 2000. *Phytocoenologia* 33: 801–818.

CARRIÓN, J. S., A. ANDRADE, K. D. BENNETT, C. NAVARRO, AND M. MUNUERA. 2001. Crossing forest thresholds: inertia and collapse in a Holocene sequence from south-central Spain. *The Holocene* 11: 635–653.

CASTRO, J., J. M. GÓMEZ, D. GARCÍA, R. ZAMORA, AND J. A. HÓDAR. 1999. Seed predation and dispersal in relict Scots pine forests in southern Spain. *Plant Ecology* 145: 115–123.

CHARLESWORTH, D., AND M. T. MORGAN. 1991. Allocation of resources to sex functions in flowering plants. *Philosophical Transactions of the Royal Society of London. Series B, Biological Sciences* 332: 91–102.

ERIKSSON, O., AND H. FRÖBORG. 1996. "Windows of opportunity" for recruitment in long-lived clonal plants: experimental studies of seedling establishment in *Vaccinium* shrubs. *Canadian Journal of Botany* 74: 1369–1374.

FAO FOREST RESOURCES DIVISION. 1989. Arid zone forestry: A guide for field technicians. FAO Conservation Guide no. 20. FAO Publications, Rome, Italy.

GALLOWAY, L. F. 2001. The effect of maternal and paternal environments on seed characters in the herbaceous plant *Campanula americana* (Campanulaceae). *American Journal of Botany* 88: 832–840.

GAO, X. J., AND F. GIORGI. 2008. Increased aridity in the Mediterranean region under greenhouse gas forcing estimated from high resolution simulations with a regional climate model. *Global and Planetary Change* 62: 195–209.

GARCÍA, D., R. ZAMORA, J. A. HÓDAR, AND J. M. GÓMEZ. 1999. Age structure of *Juniperus communis* L. in the Iberian peninsula: Conservation of remnant populations in Mediterranean mountains. *Biological Conservation* 87: 215–220.

GARCÍA, M. B., F. X. PICÓ, AND J. EHRLÉN. 2008. Life span correlates with population dynamics in perennial herbaceous plants. *American Journal of Botany* 95: 258–262.

GRACE, J. 1997. Plant water relations. *In* M. J. Crawley [ed.], Plant Ecology, 28–50. Blackwell Science, Oxford, UK.

HEGAZY, A. K., O. HAMMOUDA, J. LOVETT-DOUST, AND N. H. GOMAA. 2008. Population dynamics of *Moringa peregrina* along altitudinal gradient in the northwestern sector of the Red Sea. *Journal of Arid Environments* 72: 1537–1551.

HELENURM, K., AND B. A. SCHAAL. 1996. Genetic and maternal effects on offspring fitness in *Lupinus texensis* (Fabaceae). *American Journal of Botany* 83: 1596–1608.

KALISZ, S. 1989. Fitness consequences of mating system, seed weight, and emergence date in a winter annual, *Collinsia verna. Evolution; International Journal of Organic Evolution* 43: 1263–1272.

KASSAS, M. 1953. Landforms and plant cover in the Egyptian desert. *Bulletin de la Société de Géographie d'Egypte* 26: 193–205.

LLORET, F., J. PEÑUELAS, P. PRIETO, L. LLORENS, AND M. ESTIARTE. 2009. Plant community changes induced by experimental climate change: Seedling and adult species composition. *Perspectives in Plant Ecology, Evolution and Systematics* 11: 53–63.

LUBCZYNSKI, M. W. 2009. The hydrogeological role of trees in water-limited environments. *Hydrogeology Journal* 17: 247–259.

MILLER, D., S. R. ARCHER, S. F. ZITZER, AND M. T. LONGNECKER. 2001. Annual rainfall, topoedaphic heterogeneity and growth of an arid land tree (*Prosopis glandulosa*). *Journal of Arid Environments* 48: 23–33.

MILLINGTON, A. C., AND K. PYE. 1994. Biogeographical and geomorphological perspectives on environmental change in drylands. *In* A.C. Millington and K. Pye [Eds.], Environmental Change in Drylands: Biogeographical and Geomorphological Perspectives, 427–441. Wiley, Chichester, UK.

MINISTRY OF CIVIL AVIATION. 1975. Climatological normals for the Arab Republic of Egypt up to 1975. Meteorological Authority, Cairo, Egypt.

MONTALVO, A. M. 1994. Inbreeding depression and maternal effects in *Aquilegia caerulea*, a partially selfing plant. *Ecology* 75: 2395–2409.

MUNYANZIZA, E., AND K. A. YONGABI. 2007. *Moringa peregrina* (Forssk.) Fiori. *In*: H.A.M. van der Vossen and G.S. Mkamilo [Eds.]. PROTA 14: Vegetable oils/Oléagineux [CD-Rom], PROTA, Wageningen, Netherlands.

MÜNZBERGOVÁ, Z., AND D. WARD. 2002. *Acacia* trees as keystone species in the Negev desert ecosystems. *Journal of Vegetation Science* 13: 227–236.

PICÓ, F. X., N. J. OUBORG, AND J. M. VAN GROENENDAEL. 2003. Fitness traits and dispersal ability in the herb *Tragopogon pratensis* (Asteraceae): decoupling the role of inbreeding depression and maternal effects. *Plant Biology* 5: 522–530.

PICÓ, F. X., AND M. RIBA. 2002. Regional-scale demography of *Ramonda myconi*: remnant population dynamics in a preglacial relict species. *Plant Ecology* 161: 1–13.

RADDAD, E. Y. 2007. Ecophysiological and genetic variation in seedling traits and in first-year field performance of eight *Acacia senegal* provenances in the Blue Nile, Sudan. *New Forests* 34: 207–222.

ROACH, D. A., AND R. WULFF. 1987. Maternal effects in plants. *Annual Review of Ecology and Systematics* 18: 209–235.

SEAGER, R., M. TING, I. HELD, Y. KUSHNIR, J. LU, G. VECCHI, H. P. HUANG, ET AL. 2007. Model projections of an imminent transition to a more arid climate in southwestern North America. *Science* 316: 1181–1184.

SHER, A. A., K. WIEGAND, AND D. WARD. 2010. Do *Acacia* and *Tamarix* trees compete for water in the Negev desert? *Journal of Arid Environments* 74: 338–343.

SOLOMON, S., G. K. PLATTNER, R. KNUTTI, AND P. FRIEDLINGSTEIN. 2009. Irreversible climate change due to carbon dioxide emissions. *Proceedings of the National Academy of Sciences, USA* 106: 1704–1709.

STAVE, J., G. OBA, A. B. ERIKSEN, I. NORDAL, AND N. C. STENSETH. 2005. Seedling growth of *Acacia tortilis* and *Faidherbia albida* in response to simulated groundwater tables. *Forest Ecology and Management* 212: 367–375.

STEBBINS JR., G. L. 1952. Aridity as a stimulus to evolution. *American Naturalist* 86: 33–44.

SUSKO, D. J., AND L. LOVETT-DOUST. 2000. Patterns of seed mass variation and their implications on seedling traits in *Alliaria petiolata* (Brassicaceae). *American Journal of Botany* 87: 56–66.

VAUGHTON, G., AND M. RAMSEY. 1997. Seed mass variation in the shrub *Banksia spinulosa* (Proteaceae): resource constraints and pollen source effects. *International Journal of Plant Sciences* 158: 424–431.

WEBER, J. C., M. LARWANOU, A. ABASSE, AND A. KALINGANIRE. 2008. Growth and survival of *Prosopis africana* provenances tested in Niger and related to rainfall gradients in the West African Sahel. *Forest Ecology and Management* 256: 585–592.