



Seed germination and early development in seedlings of *Noveloa coulteriana* (Podostemaceae)



Guillermo Castillo, Judith Márquez-Guzmán, Margarita Collazo-Ortega*

Laboratorio de Desarrollo en Plantas, Departamento de Biología Comparada, Facultad de Ciencias, Universidad Nacional Autónoma de México, Avenida Universidad No. 3000, Ciudad Universitaria, Coyoacán, Distrito Federal, 04510, México, Mexico

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ABSTRACT

Unlike other aquatic plants, in Podostemaceae sexual reproduction is the primary mode of reproduction. Thus, germination and seedling establishment are essential processes in the life history of these plants, as they determine their distribution, survival, and abundance. Few studies have examined germination and early seedling development of the Mexican species of this family. In this paper, we experimentally evaluated the influence of light quality (white, red, far red, and darkness), storage time (three months, six months, and 10 years) and temperature (constant 25 °C and alternate 15–25 °C) on *Noveloa coulteriana* germination. Seeds were positive photoblastic, and showed high germination capacity in white and red light treatments (>80%). In contrast to previously studied Mexican podostemads, *N. coulteriana* seeds are recalcitrant. Seeds were also thermoblastic; germination rate was slower in alternate temperature compared to constant temperature. Additionally, using electron microscopy, we observed *ex situ* seedling development during one month (until its senescence). Micromorphologically, *N. coulteriana* seedlings showed the characteristic developmental pattern of the subfamily Podostemoideae, where the embryonic shoot and root meristems are lost. Our results indicate that environmental factors such as light quality or temperature fluctuation modify seed germination of *N. coulteriana* and may play an important role in the reestablishment of natural populations.

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1. Introduction

Podostemaceae is the largest family of strictly aquatic angiosperms (Philbrick and Novelo, 2004), including 48–50 genera and more than 270 species (Khosla et al., 2000; Philbrick and Novelo, 2004). There are 21 genera and 135 species in the Americas, most of them belonging to the subfamily Podostemoideae. Their distribution is restricted to fast-flowing rivers and waterfalls with water temperatures ranging from 14 to 27 °C in tropical regions. Commonly these rivers are oligotrophic and contaminant-free, although it has been mentioned that certain species of this family can grow in moderately polluted rivers in México (Quiroz et al., 1997). The podostemad life cycle is closely related to the water level of the rivers they inhabit (Philbrick and Novelo, 2004). They grow firmly attached to rocks that are splashed regularly by water. During the rainy season when the water level is high, vegetative structures grow submerged and anchored to bedrock; later, when the water level decreases during the dry season, reproductive structures emerge (Philbrick and Novelo, 1995). At this point

flowering and pollination occur and fruits and seeds are formed; later, these seeds will reestablish the population during the next rainy season (Luna, 2006).

Unlike most aquatic angiosperms, which tend to reproduce vegetatively (Grace, 1993), sexual reproduction and seed germination are fundamental processes in the life history of Podostemaceae, as they determine their dispersal, survival, and abundance (Philbrick and Novelo, 2004; Reyes-Ortega et al., 2009). Despite this, there are few studies on reproductive biology that includes seed production, germination, and seedling development in Podostemaceae (Díaz-Vásquez, 2012). Seed germination is regulated by several intrinsic factors such as dormancy, and by external factors such as light quality and temperature (Baskin and Baskin, 2001). Seed response to light is mediated mainly by the phytochrome (Pr/Pfr), which is a red (R) and far red light (FR) photoreceptor in plants (Sawada et al., 2008; Kami et al., 2010). Absorption of red light (± 660 nm) converts the inactive form of the phytochrome Pr to its active form Pfr (promoting or inhibiting germination), whereas the absorption of far red light (± 730 nm) converts Pfr back to Pr (Baskin and Baskin, 2001). According to their response to light, seeds have been classified as positive photoblastic if light triggers germination and as negative photoblastic if light inhibits germination. If germination is unrelated to light, seeds are considered non-photoblastic (Baskin and Baskin, 2001). Temperature may also have an effect on the

* Corresponding author. Tel.: +52 55 5622 4916; fax: +52 55 5622 4828.

E-mail addresses: mague.collazo@ciencias.unam.mx, mague49@hotmail.com (M. Collazo-Ortega).

endogenous chemical mechanisms of germination (e.g., ABA/GA hormone balance, phytochrome activity), modifying germination rate and/or germination lag time (Baskin and Baskin, 2001). Germination of a given species occurs in a temperature range related to the habitat they live in (thermic window) and the maturation stage of the seed embryo. Seeds whose germination is regulated by temperature are considered thermoblastic (Orozco-Segovia and Sánchez-Coronado, *in press*). In addition, storage time can affect seed viability; according to their tolerance to dryness, seeds are classified as recalcitrant if they do not survive drying and/or freezing and germinate immediately after been released, or as orthodox when they can resist drying and/or freezing and remain viable in a seed bank (Hong and Ellis, 1996).

Studies of germination in controlled laboratory conditions are scarce in Podostemaceae, and most of them were performed under *in vitro* conditions to obtain seedlings for developmental and taxonomic studies (Mohan Ram and Sehgal, 2001; Kita and Kato, 2005; Koi and Kato, 2010; Katayama et al., 2011; Koi et al., 2012). Philbrick and Novelo (1994) studied seed germination of four Mexican species: *Marathrum foeniculaceum* (including *Marathrum haenkeanum* and *Marathrum rubrum*), *Noveloa coulteriana* (syn. *Oserya coulteriana*), *Marathrum plumosum* (syn. *Vanroyenella plumosa*), and *Tristicha trifaria* (for name changes, see Tippery et al., 2011). All species showed high germination (>95%) after being stored for 18 months. However, this work did not test germination requirements (temperature and light quality) for these species. Recently, Reyes-Ortega et al. (2009) showed that seeds of *M. foeniculaceum* (including *M. rubrum* and *M. schiedeanum*) are positive photoblastic and that germination rate is highest at 25 °C.

Podostemaceae morphology is also particular and often controversial (Jäger-Zürn, 2009). According to Cook and Rutishauser (2007), podostemads seedlings have two cotyledons and a plumule that usually stops its growth after the appearance of some appendages (e.g., *Indostristicha ramosissima*). In these species, development continues by lateral endogenous or exogenous outgrowths of the hypocotyl (commonly named secondary or adventitious roots). These structures play a central role in the fixation of the plant to the substrate (Sehgal et al., 2002; Eckardt and Baum, 2010). However, in other species (e.g., of genera *Hydrobryum*), there is no plumular activity, and in New World taxa (e.g., *Apinagia* spp., *Mourera fluviatilis*, and *Weddellina squamulosa*) the plumule gives rise to vigorous shoots.

This morphological controversy is due in part to incomplete knowledge about the developmental stages from seedlings to adult plants. Until now, any attempt to grow Podostemaceae seedlings from seeds outside their natural habitats has failed, and even *ex situ* culture was impossible until recently, when the *in vitro* culture techniques by Sehgal et al. (1993) were developed. Since then, various podostemads have been cultivated *in vitro* by Indian (Mohan Ram and Sehgal, 1997, 2001) and Japanese researchers (Imaichi et al., 2004; Kita and Kato, 2005; Koi and Kato, 2010). Recent research incorporating these *in vitro* techniques has attributed the unusual horizontal body plan of Podostemaceae to the loss of embryonic shoot and root meristems, converting the growth direction from vertical to a horizontal body plan (Katayama et al., 2010, 2011).

In this paper, we studied seed germination and early development of the Mexican podostemad *Noveloa coulteriana*. Particularly, we evaluated the effect of (i) light quality (white, red, far-red) and darkness, (ii) temperature fluctuation (constant vs. alternating), and (iii) storage time on seed germination. Additionally, we described the early morphology of *N. coulteriana* seedlings by means of scanning electron microscopy. *N. coulteriana* is endemic to certain rivers in Mexico and subject to special protection under Mexican law (NOM-059-SEMARNAT-2010, *Secretaría del*

Medio Ambiente y Recursos Naturales, 2010). Previous studies with Mexican species have shown that *N. coulteriana* is non-dormant, with high percentages of seed germination. However, germination requirements for this species remained unknown (Philbrick and Novelo, 1994).

2. Method

2.1. Study system

Noveloa coulteriana (Tul.) C. Philbrick (syn. *Oserya coulteriana*) is a small herb, annual or perennial, with prostrated and flattened roots, 15 cm long and 0.5–1.8 mm in diameter (Philbrick and Novelo, 1997). It is endemic to Mexico (*Secretaría del Medio Ambiente y Recursos Naturales*, 2010) and is distributed along the Pacific Coast from Sonora to Guerrero and Baja California Sur, ranging from sea level to 300 m.a.s.l. (Philbrick and Novelo, 1997). *N. coulteriana* usually inhabits unpolluted rivers (Quiroz et al., 1997). However, most of the rivers this species inhabits in Jalisco (México) are exposed to some degree of anthropogenic disturbance (personal observation).

2.2. Plant material

Based on *N. coulteriana* abundance, we collected fruits from the Horcones River, located 28 km south of Puerto Vallarta (Jalisco), in the municipality of Cabo Corrientes (20°27'45" N, 105°17'30" W) in México. Mature fruits (from the same flowering season) were randomly collected from plants growing on 20 different rocks in November 2005 and February 2006. In the field, ±8 days after pollination, fruits show the external (morphology and color) characteristics of a mature fruit. After ±25 days, the seeds are viable and fruit dehiscence occurs (Luna, 2006). Thus, the age of collected seeds was less than one month in both the November 2005 and February 2006 collections. (We discarded immature and open fruits.) Seeds were air-dried and stored in paper bags at 22 °C in the dark in the laboratory until the germination experiment was begun. We also used seeds collected by Alejandro Novelo and Thomas Philbrick in the Horcones River during 1997 and donated by Alejandro Novelo. Thus, we used three collections with different storage time (three months, six months and 10 years) in the germination experiments.

2.3. Seed germination experiment

Germination experiments were done in May 2006. Treatments were combinations of temperature timing and light quality. Temperature treatments were either constant (25 °C) or alternating temperature (15/25 °C). In order to determine the photoblastic characteristics of seeds, we used the following light quality treatments: red (R) and far red light (FR), white light (WL), and darkness. For each treatment, three replicates of 25 seeds were sown in Petri dishes that were filled with non-saline water. Seeds were germinated in a Biotronette 84 germination chamber (Lab-line Inc.; IL, USA). For the WL treatment, Petri dishes were placed in the germination chamber without a filter (R: FR = 1.73), for the R and FR treatments, seeds were placed in Plexiglas filter boxes (Red treatment, R: FR = 5.22, Far Red treatment, R: FR = 0.05). Total dark was achieved by wrapping the Petri dishes with aluminum foil. The photoperiod used in all treatments was 16/8 h. Seeds germinated in WL were counted daily with the help of a stereoscopic microscope until germination was depleted. For the other treatments, only the final number of germinated seeds was counted in order to avoid interruption of the treatments. The seed germination experiment stopped when germination in WL treatment reached asymptote (16 days after germination, DAG). We estimated final germination

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