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Original article

The role of fleshy pericarp in seed germination and dispersal under flooded conditions in three wetland forest species

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ABSTRACT

In flooded habitats, inundations affect important forest regeneration processes, such as seed dispersal and germination. The main seed dispersal mechanism used by species in Austral South American temperate swamp and riparian forests is endozoochory, which releases seeds from the fleshy pericarp. Endozoochory could be favorable or unfavorable in wetland habitats, since this mechanism exposes seeds directly to water and can, in some cases, be detrimental to germination. In this study, we studied whether or not the fleshy pericarp favors germination after the flooding period's end. Furthermore, we quantified if the number of days which the fruit was found to be floating related to its germination success. We used the seeds of three common fleshy fruit species of flooded habitats from southern Chile, the trees *Luma apiculata* and *Rhaphithamnus spinosus*, and the vine *Luzuriaga radicans*. We simulated flooding periods of 7, 15, 30 and 45 days submerging seeds, with and without pericarps, in water. We found that the pericarp's presence significantly increased *Luma*'s germination success and significantly decreased that of *Luzuriaga*. The germination of *Rhaphithamnus* was low after periods of flooding in both seed treatments, with no significant differences found between them. The fruits could float for an average of one to four weeks, depending on the species, which did not relate to their germination success. These results show that germination was affected by the presence of fleshy pericarps in flooded conditions and furthermore, that flotation allows for hydrochory from one week to one month. We suggest that in swamp forests multiple seed dispersal mechanisms are advantageous, especially for fleshy-fruited species.

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1. Introduction

Many tree species in wetland forests disperse their seeds during the flooding season (Kubitzki and Ziburski, 1994; Schneider and Sharitz, 1988), with some seeds falling in the water after release from the parent plant. Continuous submersion in water produces changes in seed viability and germination (Guo et al., 1998; Lobo and Joly, 1998; Parolin et al., 2003; Walls et al., 2005). Many seeds from wetland forest species have evolved tolerance to prolonged periods underwater, employing different strategies to avoid anoxia produced by submersion (Parolin, 2001; Parolin et al., 2003). Different responses to flooding have been described in tropical and temperate forests, such as increased or decreased seed viability as

well as delayed or even accelerated seed germination (Ferreira et al., 2007; Parolin, 2001; Rudinger and Dounavi, 2008; Walls et al., 2005). Seed responses vary with flooding duration, which determines seed germination patterns and the establishment success of seedlings and future wetland forest composition (Parolin et al., 2004; Scarano, 1998; Walls et al., 2005).

The presence of external structures (e.g., waterproof tissues, air cavities, appendages, hairs, pericarp or wings) of fruits and seeds can provide certain advantages when seeds drop into the water. These structures can permit flotation and movement of propagules by water (hydrochory), but they can also be related to dispersal by wind (anemochory) and animals (zoochory) (Parolin et al., 2010). These floating structures can allow seeds to avoid negative submersion impacts, especially at times that are not favorable to seed germination (Kubitzki and Ziburski, 1994; López, 2001; Parolin et al., 2003). Although some structures may not have evolved for reproduction through seeds in water-flooded habitat, they may favor seed dispersal and seed survival in flooded habitats (Cousens et al., 2008; Van der Pijl, 1972), by providing flotation and long distance dispersal

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events (Nilsson et al., 2010) or decreasing time spent underwater (López, 2001; Oliveira-Wittmann et al., 2007). Flotation of ripe fleshy fruits, such as berries and drupes, can be achieved through spongy or woody tissues present in the pericarp (Kubitzki and Ziburski, 1994; López, 2001). Moreover, the fleshy layer or pericarp can act as a mechanical barrier to prevent water imbibition, delay germination, and extend seed survival (see Cipollini and Levey, 1997; Robertson et al., 2006).

In swamp and riparian forests in southern Chile, seeds may fall into the water without their fleshy pericarp due to frugivore activity (Armesto et al., 1987; Figueroa and Castro, 2002). Fruits can also fall simply through gravity (Donoso, 2006), in which case the seed remains enclosed by the pericarp when it reaches the water. Whether or not seeds fall to the water with their pericarp intact may have different effects on later seed germination and therefore influence subsequent establishment of seedlings and the future composition of wetland forests.

Accordingly, our hypothesis is that seeds from swamp trees, which fall into the water without pericarp (e.g., dispersed by avian frugivores), should present different seed germination responses than seeds contained inside the fleshy fruits dispersed by gravity (barochory). Furthermore, flotation capability of the fruit with intact pericarp may prevent the complete submersion of the fruit favoring seed germination success and facilitating hydrochory (López, 2001). We assessed the role of the fleshy pericarp in protecting and permitting flotation of seeds during the flooding season in three common woody species inhabiting wetland forests in southern Chile. The objectives of this study were: 1 - To determine the effect of flooding duration on the final percentage and the timing of seed germination over time for seeds with and without pericarp; and, 2 - To determine the flotation capacity of the fruit and its possible relationship with seed germination percentage.

2. Materials and methods

We quantified seed germination of three plant species that have ripe fleshy fruits during the austral flooding season (austral autumn and winter, i.e. May–September): two small trees, *Luma apiculata* (D.C.) Burret (Myrtaceae) and *Rhaphithamnus spinosus* (Juss.) Moldenke (Verbenaceae), and one vine *Luzuriaga radicans* Ruiz et Pav (Philesiaceae). *L. apiculata* and *L. radicans* are as common in swamp as in upland evergreen forests, but *R. spinosus* is less common in swamp forest (Ramírez et al., 1983).

The fruits of *L. apiculata* are 10 mm in diameter, black and contain between three and six seeds. The fruits of *R. spinosus* measured 12 mm on average, are blue and contain two seeds. The fruits of *L. radicans* have a diameter of 16.4 mm on average, are orange and have four seeds each (Armesto et al., 1987). *L. apiculata* fruits are ripe from March to July, *L. radicans* between December and June and *R. spinosus* from January to July (Smith-Ramírez and Armesto, 1994).

Fruits were collected in June 2008 from swamp forests at the Universidad Austral de Chile's Fundo San Martín Experimental Forests (39°48' S, 73°14' W). Fruits were taken from branches of between 10 or 15 individuals per species. In the case of the vine *L. radicans*, an individual was defined as all branches growing on the same host tree. The fruits were stored in airtight bags and refrigerated (4 °C) for one to two days before starting the experiments. The fruits collected were divided into two groups: fruits that were left with their pericarp intact and fruits from which we manually extracted the seeds.

2.1. Flooding experiment

Seeds with (WP) and without pericarp (WOP) were exposed to periods of 7, 15, 31 or 45 days of simulated flooding, plus a control

group of seeds without pericarp which were sown directly in soil with water at field capacity. Flooding conditions were simulated inside individual plastic containers of 300 cc. Sixty fruits, seeds WP, were placed individually in containers filled with rainwater collected from Valdivia for each of the periods of flooding. After each period of flooding, one seed was extracted manually from inside the fruit and planted in soil inside the same container, without water. Fifty seeds WOP were sown individually in soil placed inside a container filled with rainwater for each flood period. At the end of each flooding period water was completely drained from the soil. The soil substrate used for planting was collected from a swamp located in the Arbotum of the Universidad Austral de Chile, previously sterilized (150 °C for 3 h) and sieved. Seeds in soil were watered every three days. Seed germination activity was recorded every 3 or 4 days for six months. Germination was defined as the emergence of the seedling above the soil surface (appearance of cotyledons, hypocotyl or root). Furthermore, flotation of seed WP was recorded every four days in the 45-day flooding treatment. The flooding experiments were mounted outdoors during the austral flooding season (May to September), exposed to natural temperature variations. A tin roof provided protection from rain and direct sunlight.

2.2. Data analyses

For each species and treatment (WP and WOP), a logistic regression was conducted with data on germinated and non-germinated seeds as the dependent binomial variable and flooding duration as the independent categorical variable, with the control group as the reference level. In addition, for each species, we compare the germination between seeds WP and WOP during the same flooding period by means of Chi-square tests, with the frequency of germinated and non-germinated seeds in both WP and WOP. In the case of *R. spinosus*, we used Yates correction due to the low germination.

The effect of flooding period on the progress of germination of seeds WP or WOP was analyzed using the Kruskal–Wallis test, since the data were non-parametric. Mann–Whitney tests were performed to compare timing of seed germination among seeds WP and WOP in the same flooding period. In these analyses we considered the time 0 when the seed was sown in soil or fruit was in contact with the water (aquatic dispersal event).

A logistic regression analysis assessed the relationship between the period of floatation and germination success. For this, we used the number of days that fruits were observed floating (seeds WP) in the 45 days flooding treatment, and determined whether the seeds in the fruit did or did not germinate. Sample sizes used for this analysis were 53, 49 and 60, for *L. apiculata*, *R. spinosus* and *L. radicans* respectively, because some seeds in the fruits were damaged by insects.

3. Results

3.1. Seed germination differences among flooding periods

The numbers of days that *L. apiculata* seeds WOP remained in water in three flooding treatments (15, 31 and 45 days) did not affect their germination percentage in comparison to the control (not submerged), (15 days: *Estimate coefficient* (*E. c.*) = 0.05, *Wald* = 0.31, *P* = 0.87; 31 days: *E. c.* = -0.67, *Wald* = 3.25, *P* = 0.07; 45 days: *E. c.* = 0.05, *Wald* = 0.26, *P* = 0.87), except for the seven-day treatment (Fig. 1a). For the seven-day flooding period, seed germination percentage was higher than for other treatments (*E. c.* = 1.074, *Wald* = 15.30, *P* < 0.001; Fig. 1a). For *L. apiculata* seeds contained inside the fruit (WP), the number of days that they remained underwater did not affect their germination percentage

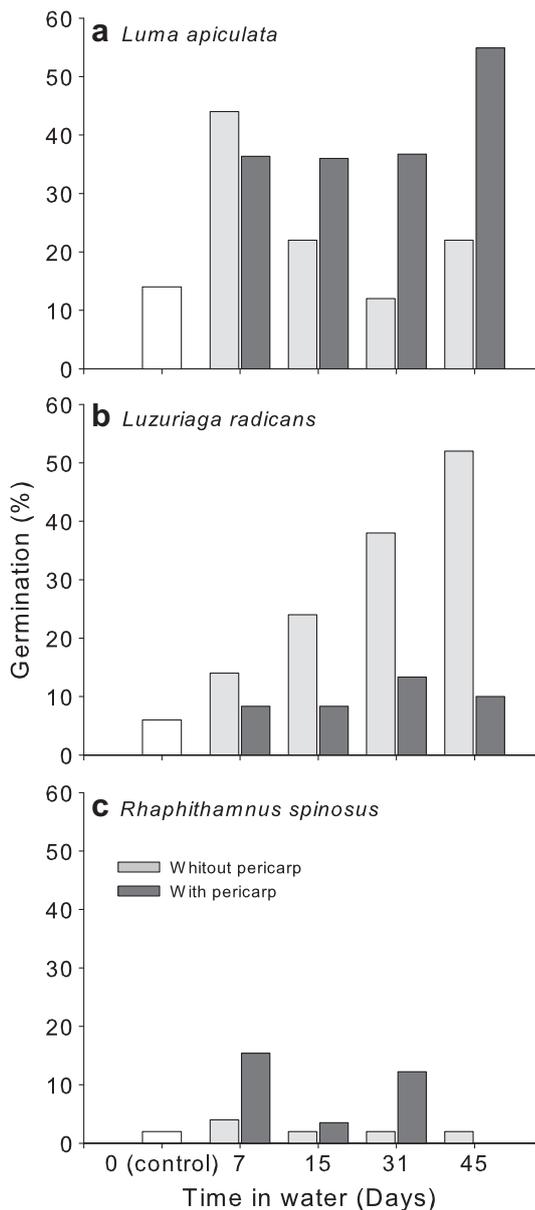


Fig. 1. Seed germination percentage of three wetland forest species, a) *Luma apiculata*, b) *Luzuriaga radicans* y c) *Rhaphithamnus spinosus*, after seeds with and without pericarp were subjected to different flooding periods.

in comparison to the control, except for the 45-day treatment, which caused an increase in seed germination percentage ($E. c. = 0.86$, $Wald = 10.74$, $P = 0.001$; Fig. 1a). Seed germination percentages for seeds WOP ranged from 12 to 44%, whereas the range was 36–55% for seeds WP (Fig. 1a).

The 7 and 15 days treatments in the case of *L. radicans* seeds (WOP) did not affect their germination percentage in comparison to the control (7 days: $E. c. = -0.59$, $Wald = 2.64$, $P = 0.10$; 15 days: $E. c. = 0.07$, $Wald = 0.05$, $P < 0.81$), but germination success was significantly enhanced in comparison to the control by the 31 and 45 days of flooding treatments ($E. c. = 0.74$, $Wald = 6.56$, $P = 0.01$) ($E. c. = 1.31$, $Wald = 21.34$, $P < 0.001$; Fig. 1b). On the other hand, the number of days that *L. radicans* seeds WP remained underwater did not affect their germination percentage in comparison to the control ($Wald = 1.92$, $df = 4$, $P = 0.75$; Fig. 1b). Seed germination percentages for seeds WOP ranged from 14 to 52%, whereas the range was between 8 and 10% for seeds WP (Fig. 1b).

The number of days that *R. spinosus* seeds WOP and WP remained underwater did not significantly affect their germination percentage in comparison to the control ($Wald = 76.35$, $df = 4$, $P = 0.96$ and $Wald = 7.10$, $df = 4$, $P = 0.13$, respectively; Fig. 1c). Seed germination percentages for seeds WOP ranged between 2 and 4%, whereas the range was between 0 and 15% for seeds WP (Fig. 1c).

3.2. Seed germination differences between seeds with and without pericarp

The germination of *L. apiculata* seeds WOP submerged for 7 and 15 days did not differ significantly from the germination percentage of seeds WP ($X^2 = 0.57$, $P = 0.45$ and $X^2 = 2.38$, $P = 0.12$, respectively). In the 30 and 45 days treatments, however, seeds WP had a significantly higher germination percentage than seeds WOP ($X^2 = 8.24$, $P = 0.004$ and $X^2 = 11.53$, $P < 0.001$, respectively; Fig. 1a).

The germination percentage of *L. radicans* seeds WOP in the seven days treatment did not differ from that of seeds WP ($X^2 = 0.9$, $P = 0.34$). For the 15, 31 and 45 days of flooding treatment, however, seeds WP had lower germination percentages than the seeds WOP ($X^2 = 5.12$, $P = 0.23$, $X^2 = 8.96$, $P = 0.002$ and $X^2 = 23.32$, $P < 0.001$, respectively; Fig. 1b).

The germination percentage of *R. spinosus* seeds WP and WOP were not statistically different for any flooding treatment (7 days: $X^2 = 2.56$, $P = 0.1$; 15 days: $X^2 = 0.1$, $P = 0.91$, 31 days: $X^2 = 2.55$, $P = 0.11$; 45 days: $X^2 = 0.1$, $P = 0.93$. Fig. 1c). *R. spinosus* showed the lowest germination rate being between 3 and 15% (Fig. 1c).

3.3. Timing of seed germination

The timing of germination of *L. apiculata* WOP was only statistically different between the 15 and 45-day ($H_{(4,57)} = 12.30$, $P = 0.015$, Multiple comparisons, $P = 0.02$; Table 1; Fig. 2a). The *L. apiculata* seeds WP did not present differences in the times of seed germination for any treatments, including the control ($H_{(4,87)} = 4.94$, $P = 0.30$; Table 1; Fig. 2a).

Comparing the timing of seed germination among seeds WP and WOP shows that under the 7 and 15-day flooding treatment *L. apiculata* seeds WP began to germinate on average 17 and 26 days before than the seeds WOP, respectively ($U = 99$, $P = 0.002$ and $U = 45$, $P = 0.014$; Table 1; Fig. 2a). In contrast, for the 31 and 45-day flooding treatments there were no differences in the timing of seed germination between seeds WP or WOP ($U = 42.5$, $P = 0.44$ and $U = 116.5$, $P = 0.24$; Table 1; Fig. 2a).

The seeds of *L. radicans* WOP did not show differences in timing of germination among treatments, including the control ($H_{(4,27)} = 6.87$, $P = 0.14$). However, *L. radicans* seeds WP delayed seed germination under flooding treatments ($H_{(4,27)} = 18.28$, $P = 0.001$). In two groups, control and 7-day flooding treatment, seeds germinated on average 50 and 43 days, respectively, before seeds subjected to 45-day flooding (Multiple comparisons, $P = 0.012$ and $P = 0.007$) (Table 1; Fig. 2b). Further differences in the timing of seed germination were found among the 15-day ($U = 4$, $P = 0.006$), 31-day ($U = 1$, $P < 0.001$) and 45-day ($U = 0$, $P < 0.001$) treatments between *L. radicans* seeds WP and WOP (Fig. 2b).

In *R. spinosus*, timing of germination did not differ significantly among treatments for seeds WP ($H_{(4,6)} = 3.14$, $P = 0.53$) or WOP ($H_{(3,17)} = 6.10$, $P = 0.11$), including control seeds (Table 1; Fig. 2c). In the seven-day flooding treatment, the seeds WP germinated later in comparison to the seeds WOP (an average delay of 23 days, $U = 0$, $P = 0.035$; Table 1). We found no significant differences between seeds WP and WOP for other flooding treatments (Table 1; Fig. 2c).

Table 1

Times of seed germination for three species subjected to different experimental flooding treatments (0 (control) to 45 days), comparing seeds with (WP) and without pericarp (WOP). *n* is number of germinated seeds; ASG ± SD = average number of days that start seed germination ± standard deviation; Range = number of days of maximum and minimum timing of germination; Different characters show significant differences ($P < 0.05$) in seeds WP or WOP, between the flooding treatments; Asterisks show significant differences ($P < 0.05$) in the same flooding period between seeds WOP and WP.

Species	Treatments		<i>n</i>	ASG ± SD	Range	
	Flooding period (days)	Pericarp				
<i>Luma apiculata</i>	Control		7	83 ± 41	45–170	
		7*	WOP	22	76 ± 22	45–113
	15*	WP	16	93 ± 25	52–154	
		WOP ^a	11	68 ± 38	45–170	
		WP	18	94 ± 34	52–151	
		WOP	6	89 ± 21	64–128	
	31	WP	18	103 ± 33	68–176	
		WOP ^b	11	91 ± 15	81–131	
	45	WP	28	97 ± 22	64–156	
				3	151 ± 23	131–176
<i>Luzuriaga radicans</i>	Control ^a		7	138 ± 35	92–187	
		7	WOP	5	163 ± 8	159–178
	15*	WOP	12	136 ± 34	86–176	
		WP	5	188 ± 11	169–195	
	31*	WOP	19	133 ± 27	85–180	
		WP	8	196 ± 12	178–207	
	45*	WOP	26	153 ± 18	115–176	
		WP ^b	6	210 ± 18	181–232	
	<i>Rhaphithamnus spinosus</i>	Control		1	99	–
			7*	WOP	2	107 ± 16
15		WP	8	84 ± 8	72–92	
		WOP	1	99	–	
		WP	2	87 ± 3	85–89	
		WOP	1	139	–	
31		WP	6	102 ± 19	85–133	
		WOP	1	95	–	
45		WP	0	–	–	

3.4. Fruit flotation

The fruits of the vine *Luzuriaga* showed the lowest flotation ability in comparison to the other two species, with only 6 days on average and not floating fruits at 11 days (Table 2, Fig. 3). Fruits of both *L. apiculata* and *R. spinosus* were able to float for a maximum of 45 days of flooding (Table 2; Fig. 3), with an average of 13.6 days for *L. apiculata* and 29.3 days for *R. spinosus*. The length of the flotation period of the fruits did not correlate with the rates of seed germination for any species (Table 2).

4. Discussion

Our results suggest that the fleshy pericarp inhibits the effects of submergence on seed germination. Differences in germination between seeds with and without pericarp in *L. apiculata* and *L. radicans* support our hypothesis. The total germination percentage and timing were influenced by different submergence periods and pericarp presence or absence. These results indicate that seed dispersal vector can significantly influence germination when seeds fall into the water in wetland forests. In addition, fruits were able to float for several days, and, although no relationship with germination probability was determined, this characteristic may facilitate dispersal via hydrochory.

L. apiculata has recalcitrant seeds (Figueroa et al., 1996, 2004), which are characterized by fast germination when free from the pericarp in high moisture environments (Farnsworth, 2000). But when exposure to underwater extends for a prolonged time, the embryo of different types of seeds may be damaged and reduce germination rate, as it has been found by Crawford (1977), Guo et al. (1998), Walls et al. (2005) and Pérez-Ramos and Marañón (2009). In this study, *L. apiculata* seeds with pericarp showed a constant and enhanced germination percentage from increase of times underwater (7 at 45 days), in contrast to seeds without pericarp, for

which germination decreased with the length of the flooding treatment. Delayed seed germination was the only impact caused by the different lengths of times that seeds remained underwater. In fact, seeds that remained within the fruits longer germinated more rapidly (when we removed the pulp) than those seeds that were manually removed from the pericarp before flooding. If the pericarp caused an inhibition of seed germination, we would have expected a greater delay of seed germination in seeds WP.

For *L. apiculata*, the fleshy pericarp could serve as a mechanical barrier that prevents rapid seed imbibition and, possibly, premature germination, as has been proposed by Cipollini and Levey (1997) for fleshy fruits in general. Figueroa and Castro (2002) found that *L. apiculata* seeds did not germinate while they were within intact fruits. In the 45 days submersion treatment, we found water inside some *L. apiculata* fruits, and seeds extending their hypocotyls, despite being enclosed by the pericarp, suggesting that air reserves on the fruit could lead to its germination, even underwater. Despite the loss of the pericarp's inhibitory effect after 45 days of flooding, the pericarp appears advantageous to *L. apiculata* seeds under flooding, based on the higher percent germination of seeds WP compared to seeds WOP, after 45 days of flooding, and the results of previous work showing higher viability of *L. apiculata* seeds when they remained in the pericarp (Ramírez et al., 1980).

The germination percentage of *L. radicans* seeds WOP increased with flooding time. This result may be due to the fact that *L. radicans* is a monocot, with embryos completely covered by the endosperm (Rodríguez and Marticorena, 1987). When monocot seeds are exposed to hypoxia/anoxia conditions, they use the endosperm to maintain anaerobic fermentative pathways, allowing root extension (Perata et al., 1996). Thus, the loss of morphological dormancy through endosperm consumption would explain why germination increased with time underwater. This mechanism could also explain why the time of seed germination was similar among flooding treatments. When submersion periods increased,

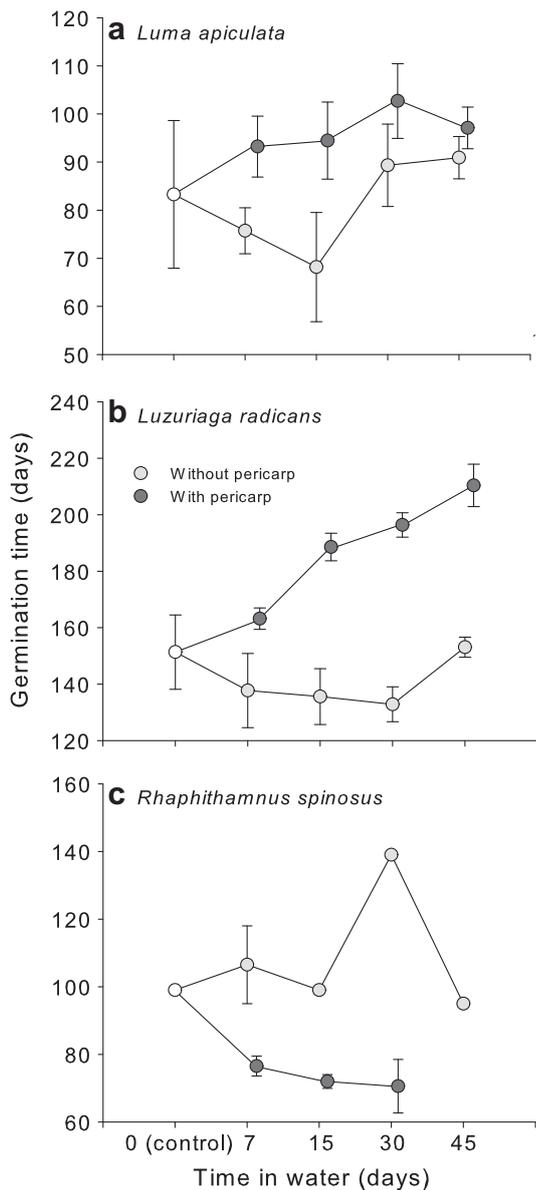


Fig. 2. Mean germination time of three wetland forest species, a) *Luma apiculata*; b) *Luzuriaga radicans*; and c) *Rhaphithamnus spinosus*, after the seeds with and without pericarp were subjected to different flooding periods. Bars are standard errors.

less time was necessary for post submergence germination due to endosperm consumption.

The increase in flooding period did not affect the germination percentage of *L. radicans* seeds WP; although germination was delayed with respect to controls. We hypothesize that when kept within the fruit, seeds are inhibited by the pericarp, which protects the seeds from the effects of submersion (see Burrows, 1995; Cipollini and Levey, 1997).

Table 2
Average and maximum flotation time of fruits of three wetland forest species and results of logistic regression between the number of days of flotation and seed germination percentage. *n* is number of fruits used to obtain the average and maximum floating time. In parentheses, the number of floating fruits actually used for logistic regression analysis that relates the buoyancy of the fruit to seed germination (see methods).

Species	<i>n</i>	Flotation days		Logistic regression		
		Mean	Maximum	Estimate coefficient	Wald	<i>P</i>
<i>Luma apiculata</i>	60 (53)	14	45	0.027	1.66	0.20
<i>Luzuriaga radicans</i>	60 (60)	6	11	-0.049	0.04	0.83
<i>Rhaphithamnus spinosus</i>	60 (49)	29	45	0.044	1.07	0.30

The low percentage of seed germination of *R. spinosus* may be due to physiological characteristics of its seeds and unrelated to flooding treatments. Cold stratification and light exposure could be important mechanisms to increase germination of *R. spinosus* seeds (Figuroa, 2003; Figuroa et al., 1996). All of the *R. spinosus* seeds kept their viability at the end of the experiment, as shown by tetrazolium tests (data not shown). Some developmental stages of *R. spinosus* (seedling or sapling) are likely to be intolerant to flooding, considering that the plants that we observed occurred in higher microsites within the swamp or at swamp forest edges but never in direct contact with water.

4.1. Consequences of being dispersed with or without pericarp

The presence of fleshy pericarp is commonly related to seed dispersal by animals (Jordano, 2000; Willson, 1991). The three species here studied have fleshy fruits, so their seeds may be principally dispersed by avian or mammal frugivores in the temperate forest of southern South America (Armesto and Rozzi, 1989; Aizen et al., 2002). However, our data suggest that other dispersal mechanisms are also possible when these species are found in wetlands, such as swamp or riparian forests. In wetland forests, gravity (barochory) causing the fleshy fruit with the seeds inside to fall off the tree or vine into the water could eventually enhance seed germination. In addition, flotation and dispersal of entire fruits or seeds by water currents (hydrochory) could be an important mechanism for the movement of the propagules along the streams, rivers or swamps (Nilsson et al., 2010).

For trees *L. apiculata* and *R. spinosus*, dispersal by barochory in wetland forests would favor germination, as seeds are protected by the pericarp from germinating underwater, maintaining their viability for several weeks. Instead, when dispersal is by a frugivore within the wetlands, the seeds will be exposed to the risk of prolonged submersion without the protection of the pulp. Birds such as the thrush *Turdus falcklandii*, or the marsupial *Dromiciops gliroides* can perform this function (Amico and Aizen, 2005; Amico et al., 2009; Figuroa and Castro, 2002; Salvande et al., 2011). For the vine *L. radicans*, we propose that endozoochory would be the most effective form of dispersal in wetland forests. *L. radicans* fruits are consumed by the rodent *Irenomys tarsalis* (Meserve et al., 1988) and *D. gliroides* (Amico et al., 2009; Armesto et al., 1987). *L. radicans* and *L. apiculata* are abundant in both upland and wetland forests (Armesto and Figuroa, 1987; Ramírez et al., 1996), which suggests that the submersed periods might not be necessary or limiting for the germination of its seeds, respectively. Furthermore, these species can reproduce vegetatively, which is a common strategy for plant propagation in flooded habitats (Deiller et al., 2003). Finally, barochory of fruits in these three species as an initial dispersal mechanism would permit hydrochory as secondary dispersal mechanism linked to fruit flotation capability. Although fishes are important frugivores and seed dispersers (ichthyochory) in temperate and neotropical wetland ecosystems (Horn et al., 2011), this is unlikely to occur in Chilean wetland forests, because the diet of fishes are based on microorganisms and small invertebrates (Habits and Victoriano, 2005; Vila et al., 2006).

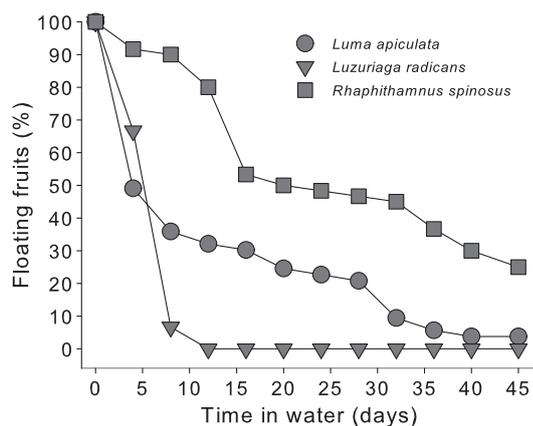


Fig. 3. Percentage of fruits that remained floating over time for three wetland forest species, *Luma apiculata*, *Luzuriaga radicans* and *Rhaphithamnus spinosus*, subjected to experimental flooding for 45 days ($n = 60$ fruits per species).

Some authors have argued that having multiple dispersal mechanisms provides an advantage for species due to an increase in the range of microhabitat types where seeds can establish (Adams et al., 2007; Oliveira-Wittmann et al., 2007). In part, the combination in sequence of barochory and hydrochory, i.e. a diplochory (Vander Wall and Longland, 2004), may be responsible for the presence of *L. apiculata*, *L. radicans* and *R. spinosus* in swamp and riparian forests. Furthermore, multiple dispersal mechanisms can compensate for the relative lack of frugivorous species in Chilean temperate forests (Armesto et al., 1996) and increase the chances of seed dispersal across the landscape.

We conclude that the fleshy pericarp of *L. apiculata* and *L. radicans* can prevent the effects of submersion on seed germination, and allow the fruits to float, promoting hydrochory. Barochory could be an additional dispersal mechanism related to hydrochory, both of which supplement dispersal by endozoochory in wetland forest habitats.

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