Flora 224 (2016) 167–171

Contents lists available at ScienceDirect

Flora

journal homepage: www.elsevier.com/locate/flora

Are birds, wind and gravity legitimate dispersers of fleshy-fruited invasive plants on Robinson Crusoe Island, Chile?

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ARTICLE INFO

Article history:
Received 20 January 2015
Received in revised form 30 June 2016
Accepted 19 July 2016
Edited by Hermann Heilmeier
Available online 21 July 2016

Keywords:
Fleshy fruits
Germination
Invasive plants
Juan Fernandez Archipelago
Seed dispersers

ABSTRACT

Although fleshy-fruited species are usually dispersed by animals and gravity, previous research shows that the fleshy fruits of invasive plants on Robinson Crusoe Island (RC) are also moved by wind. To determine whether a bird (*Turdus falcklandii*), wind, and gravity could be legitimate dispersers of fleshy fruits from the invasive plant species *Aristotelia chilensis*, *Rubus ulmifolius* and *Ugni molinae*, we carried out germination trials with seeds defecated by *T. falcklandii* and hand-cleaned in the laboratory, and added another trial in field conditions, sowing intact fruits. Whole fruits sown intact are used to represent dispersal by wind or gravity. The field trials for *A. chilensis* and *R. ulmifolius* were performed in canopy gaps and closed forests to evaluate the effect of shadow on seedling emergence. Field trials for *U. molinae* were only established in open shrubland, since this species does not occur in forests on RC. Laboratory trials showed gut-passed *A. chilensis* seeds increased the germination percentage while gut-passed seeds did not affect germination in *R. ulmifolius* and *U. molinae*. In the field, trials revealed that seeds from intact fruits germinated in a similar way to gut-passed or hand-cleaned seeds, with the exception of *U. molinae*, which did not germinate inside fruits. In all field treatments, the germination percentage of *A. chilensis* and *R. ulmifolius* was higher in the canopy gaps than under closed canopy. These results indicate that *T. falcklandii* is a legitimate disperser for the three invasive species studied on RC. Wind and gravity should also be considered legitimate dispersers of *A. chilensis* and *R. ulmifolius*. Microhabitat (i.e., canopy gaps) plays a more important role in improving the establishment of *A. chilensis* and *R. ulmifolius* than the dispersal mechanism itself.

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1. Introduction

Seed dispersal of fleshy-fruited invasive plants by vertebrates, specifically birds, is a common cause of naturalization and expansion of exotic plants that may influence the subsequent alteration of environments (Gosper et al., 2005). This phenomenon has been described on many oceanic islands (Chimera and Drake, 2010; Smith-Ramírez et al., 2013; Williams, 2006). When ingested, the vertebrate's gut produces seed coat scarification, which in some cases enhances and/or accelerates germination (Traveset, 1998; Traveset et al., 2001). Additionally, vertebrates remove the pericarp, eliminating inhibitors present in the pulp that impede or delay seed germination (Samuels and Levey, 2005).

Even though endozoochory (i.e., ingestion by vertebrates) is by far the most extensively studied dispersal mechanism for fleshy fruits, barochory (gravity-dispersed) and anemochory (wind-dispersed) are other frequent vectors to disperse fruits (Armesto et al., 2001; Guan et al., 2006; McAlpine and Jesson, 2008; Smith-Ramírez et al., 2013). When seeds of fleshy fruits are dispersed by wind or gravity they remain inside the pericarp. Seeds of some species can germinate inside the fruit, or remain viable inside the fruit until environmental conditions or other agents break the husk and pulp, but others can die if that does not happen (Figueroa and Castro, 2002; Robertson et al., 2006; Yagihashi et al., 1998, 1999, 2000). Samuels and Levey (2005) conducted a literature review of 99 articles and found only 22 studies in which germination was studied in intact fruits, a common seed fate in natural conditions. Lack of these types of germination studies, par-

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http://dx.doi.org/10.1016/j.flora.2016.07.012
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ticularly in the field, is an issue. Studies focusing solely on dispersal by vertebrates fail to take into account the role of the pulp when it is not removed by dispersal agents (i.e. in wind and gravity dispersal). Despite its potential importance to the field of ecology and restoration, there is a clear disparity between published literature relating to dispersal effectiveness of animals when compared to the obvious dearth in studies of dispersal by wind or gravity (see review in Schupp et al., 2010). Evidence supporting the role of vertebrates in dispersal and establishment is clear and should not be discounted. However, if ripe fruits are light and the wind is strong anemochory and barochory are not unusual seed dispersal vectors, and have even been found to complement dispersal by birds on Taiwan (Guan et al., 2006) and on Robinson Crusoe Island (Smith-Ramírez et al., 2013).

Robinson Crusoe Island (RC) is part of the Juan Fernandez Archipelago (JFA) in the South Pacific off the Chilean coast. The JFA is a Chilean Biosphere Reserve and one of the world's most threatened biotas (Wester, 1991). RC has been considered the island with the highest endemism per m^2 in the world (Stuessy, 1992). Flora in the JFA is going to face a marked reduction in the short term due to the expansion of introduced plant species (Dirnböck et al., 2003; Smith-Ramírez et al., 2013). The most invasive plants on RC are three fleshy-fruited shrub species: *Aristotelia chilensis* (Molina) Stuntz (Elaeocarpaceae), *Rubus ulmifolius* Schot (Rosaceae) and *Ugni molinae* Turcz. (Myrtaceae). In forests, *A. chilensis*, *R. ulmifolius,* and *U. molinae* seeds are thought to be dispersed mainly by *Turdus falcklandii* Quoy & Gaimard (Turdinae), a bird widely distributed in all habitat types on RC (Hahn et al., 2011). However, it is uncertain whether *T. falcklandii* is actually a legitimate disperser of these species. In the case of *A. chilensis* seeds, *T. falcklandii* was found to move 82.1% of the seeds out of its parental tree while 17.9% was moved by wind (Smith-Ramírez et al., 2013). Moreover, *R. ulmifolius* and *U. molinae* are dispersed by wind, but less frequently than for *A. chilensis* seeds (Smith-Ramírez et al., 2013). On the other hand, germination and seedling emergence of *A. chilensis* and *R. ulmifolius* (and probably *U. molinae*) might be affected not only by dispersal vectors, but also by the forest canopy because these are light-demanding species (Arellano-Cataldo and Smith-Ramírez, 2016).

The goal of this study was to investigate the effects of seed dispersal vectors on seed germination of the invasive fleshy fruit plants *A. chilensis, R. ulmifolius* and *U. molinae* dispersed by *T. falcklandii*, wind and gravity in laboratory and field condition experiments. We ask 1) Are the above mentioned vectors legitimate seed dispersers? 2) What are their effects on seed germination percentage? 3) Are pulp removal and microhabitat (gap vs. non-gaps) important for seedling emergence in field conditions? To determine whether wind and gravity are legitimate seed disperses, we sowed intact fruits (with pulp) in the field and evaluated seedling emergence. Here, sowing intact fruits was used as a proxy for wind and gravity. The pulp presence has been considered amply in scientific literature as an adequate indicator of seed dispersal by wind and gravity (Armesto et al., 2001; Guan et al., 2006; Iida and Nakashizuka, 1998; McAlpine and Jesson, 2008).

2. Methods

2.1. Seed collection

The seed collection took place in the middle of the fructification season of each species on RC. That was February for *A. chilensis* and *R. ulmifolius* (austral summer), and early May for *U. molinae* (austral autumn). In 2010 we collected 209 fresh *T. falcklandii* feces and around 200 fruits from *R. ulmifolius* and *A. chilensis* scrubs about 10 m apart each other. The collection of feces and fruits were made on the forest trails El Mirador de Selkirk and Plazoleta El Yunque on RC. In the field, the seeds were extracted from feces or fruits. Some of the seeds were kept at 5 °C (ca. 3 weeks) before being moved to the laboratory on the mainland and the others were used in field experiments. In May 2011 we collected 102 fresh *T. falcklandii* feces and 200 *U. molinae* fruits from Plazoleta El Yunque. *Ugni molinae* seeds were stored and transported inside feces or intact fruits to be extracted in the laboratory in order to protect their recalcitrant seeds from desiccation (Figueroa et al., 2004).

2.2. Laboratory experiments

To evaluate the effect of seed ingestion by *T. falcklandii* on the germination of *A. chilensis*, *R. ulmifolius* and *U. molinae*, a laboratory trial was conducted comparing defecated and non-defecated hand-extracted seeds. We did not perform trials with intact fruits in the laboratory. It is common to find null germination in laboratory assays because differences between the laboratory and natural environment (Robertson et al., 2006). Two hundred forty defecated and hand-cleaned seeds collected from RC were washed in a 2% chlorine solution to remove pulp residues and to prevent fungal contamination. Thereafter, 30 seeds for each treatment were laid on paper in four petri plaques, with a total of 120 defecated and hand-cleaned seeds per treatment. The seeds were placed inside a germination chamber at 20 °C with a light/darkness photoperiod of 12 h. One or two times per week the plaques were moistened until the paper was saturated.

After 372 days, little germination (no more than 10%) was obtained in *R. ulmifolius* and *A. chilensis*. This is a low germination percentage especially in comparison with similar studies published by Traveset et al. (2001) for *R. ulmifolius* and by Figueroa (2003) for *A. chilensis*. Then, we decided to expose *R. ulmifolius* and *A. chilensis* seeds to cold stratification (5 °C, for 35 days) inside plastic bags. These treatments improve germination of various *Rubus* spp. (Ellis et al., 1985) and we proceeded in a similar way with *A. chilensis*, although stratification is not imperative to improve germination levels of this species (Figueroa, 2003). Afterwards, the bags were kept at room temperature in the laboratory (mean 20 °C) without light for 60 more days. *Ugni molinae* seeds successfully germinated and did not need stratification. Germination (i.e. radicle emergence) was registered every 1–3 days during the first 4 months, and thereafter every week for 9 months. The recording time amounted to 467 days for both *A. chilensis* and *R. ulmifolius* and 322 days for *U. molinae*. Upon the final recording, tetrazolium tests and visual examination of seeds and embryos were performed.

2.3. Field experiments

To evaluate seed dispersal effects by *T. falcklandii* (seeds without pulp), wind, and gravity (seeds with pulp) in the field we conducted germination trials with defecated, non-defecated seeds and in addition intact fruits. The dormancy of seeds from intact fruits collected from the plants may be lower and the seed viability could be higher than fruits that remain on the ground or underground for weeks or months. Although there may be some differences between seeds collected on the plant vs. on soil, we decided to use seeds collected from plants in the assays (to represent wind and gravity dispersal). We then compared their germination with seeds collected in fresh feces, recognizable by the presence of fecal residue that had not been washed away by rain. Both groups of fresh seeds were sown at the same time, which had the advantage of producing comparative data.

Aristotelia chilensis and *R. ulmifolius* trials were carried out in February 2010 in the Plazoleta El Yunque (PEY) forest stand. The trials were made in canopy gaps and closed forest. We chose four forest canopy gaps in PEY (gap sizes = 110–360 m^2), and four closed

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